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A REVISED CLASSIFICATION OF THE SPIRIFERID BRACHIOPODS

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ABSTRACT

A new classification of the impunctate and punctate spiriferid brachiopods is presented. Where morphological evidence permits, ancestor-descendant relationships are discussed and indicated.

New taxa include the suborder Cyrtinidina Carter and Johnson; new families are Ulbospiriferidae Johnson and Carter, Lazutkinidae Johnson and Hou, Elymospiriferidae Johnson and Hou, Tenellodermidae Carter, Johnson, and Gourvennec, Perissothyrididae Carter, Palaeochoristitidae Carter, Skelidorygmidae Carter, Rastelligeridae Carter, Dimegelasmidae Carter, Spiropunctiferidae Carter; new subfamilies are Callispiriferinae Johnson, Eurekaspiriferinae Johnson, Branikiinae Johnson and Hou, Ulbospiriferinae Johnson and Carter, Palaeospiriferinae Carter, Johnson, and Hou, Howellellinae Johnson and Hou, Araspiriferinae Johnson, Eomartiniopsinae Carter, Elivellinae Carter, Sergospiriferinae Carter, Tangshanellinae Carter, Reticulariopsinae Gourvennec, Rhenothyridinae Gourvennec, Obesariinae Gourvennec, Eoreticulariinae Gourvennec, Quadrithyridinae Gourvennec, Martinothyridinae Carter, Toryniferinae Carter, Spinolepismatininae Carter, Paralepismatininae Carter, Rastelligerinae Carter, Dentospiriferinae Carter, Yalongiinae Carter, Pseudocyrtininae Carter, Dispiriferininae Carter, Tethyspirinae Carter, Paralaballinae Carter, and Jiangdospiriferinae Carter.

INTRODUCTION

In 1985 the organizers of the First International Congress on Brachiopods (Brest) sponsored a revision of the out-of-date brachiopod Treatise volumes. We were given the task of revising the spiriferids, impunctate and punctate. In the absence of any recent comprehensive revision and classification for this large group we submit the following preliminary classification of the spiriferid brachiopods for the examination and criticism of our colleagues. We recognize that no endeavor of this magnitude can be perfect or complete and beg the indulgence of our colleagues for any egregious errors or omissions. Now is the time to bring errors or omissions to our attention, before the Treatise goes to the press.

Since the first publication of the brachiopod volumes of the Treatise on Invertebrate Paleontology (Williams et al., 1965) a great deal of new information about spiriferid brachiopods has accrued concerning their diversity, morphology,

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distribution, and phylogenetic relationships. This is especially true for the spiriferid brachiopods. For example, in the first edition of the Treatise Pitrat (1965) recognized 187 spiriferid genera. Over 340 additional genera have been described in the intervening years, almost tripling the number of genus-level taxa. Also, numerous family-level taxon proposals have accompanied this descriptive explosion, often without discussion or written justification for the new taxa. Thus, a new evaluation of genera and their assignment to higher taxa is clearly in order.

Waterhouse (1968), Ivanova (1972), and Carter (1974) offered revised classifications for part or all of the spiriferid brachiopods soon after publication of the original Treatise volumes. These classifications are long outdated and have been emended numerous times or ignored. None has been accepted as a standard for the group.

In the following classification considerable emphasis is placed on shell structure (orders), growth form (suborders or superfamilies), internal structures (families or subfamilies), and micro-ornament (all family levels). Several possible synapomorphies are identified: taleola-like denticles in the Spiriferoidea and Paeckelmanelloidea, biramous spines in the Elythidae, the tichorhinum in the Cyrtinidae, development of a syrinx in the Syringothyridoidea, crenulation of the hingeline in the Superfamily Spondylospiroidea.

Although cladistic analysis was not performed in constructing this classification, it is hoped that it reflects the phylogeny of the spiriferids to a large degree. Carlson (1991), in a phylogenetic study of the brachiopod superfamilies, pointed out that the spiriferids, as classified in the 1965 Treatise, were not monophyletic and did not comprise a clade. She is presently reanalyzing this group using some of the information provided here.

Order Spiriferida Waagen, 1883

[*nom. correct.* Moore, Lalicker, and Fischer, 1952, p. 221
(*pro* order Spiriferacea Kuhn, 1949, p. 104;
nom. transl. ex suborder Spiriferacea Waagen, 1883, p. 447),
emend. Carter, Johnson, Gourvennec, and Hou, herein]

Diagnosis.—Generally biconvex; generally transverse with moderately wide to extended straight hingeline; ribbing very fine to coarse; small dorsal and larger ventral interareas always developed; spiralia directed laterally or posterolaterally with primary lamellae parallel and close to sagittal plane; jugum absent; shell substance impunctate.

Discussion.—The Order Spiriferida comprises the impunctate strophic brachiopods with a spiral brachidium and ranges from the Upper Ordovician to the Upper Permian. The oldest suborder, Spiriferidina Waagen, 1883, is represented in the Lower Paleozoic by eospiriferid genera such as *Eospirifer* and *Macropleura* that bear a capillate shell fabric and a simple interior with dental and crural plates and lack a ctenophoridium. Several authors (Rudwick, 1970; Ivanova, 1972) have suggested derivation of the order from an impunctate strophic orthid based on general morphology and age of first appearance. We tend to agree with this suggestion but cannot with confidence propose a likely intermediate ancestor. Gourvennec and Mélou (1990) recently demonstrated the similarity between the micro-ornament of the Upper Ordovician orthid genus *Ptychopleurella* and that of the spiriferid genus *Hysterolites.* However, this similarity could be accounted for by convergent or parallel evolution.

Rong et al. (1994) recently described a Late Ordovician (mid-Ashgill) species of *Eospirifer* from eastern China. This primitive species lacks crural plates and has very simple posterior cardinalia, quite unlike any known orthid. Furthermore, "spiriferoid" orthids such as *Platystrophia* or *Mcewanella* are not known from any of the areas where primitive eospiriferids have been recovered. Although the brachidium is not known for these early Chinese eospiriferids the simple cardinalia are reminiscent of some early atrypids and the possibility remains that the impunctate spiriferids may have been derived from the atrypids, not the orthids. It can be seen from these discoveries that more evidence is needed to ascertain the true ancestors of the spiriferids.

The Devonian history of the Spiriferidina is one of proliferation and diversity exemplified by the superfamilies Spinelloidea and Theodossioidea, lacking a delthyrial plate, and the Cyrtospiriferoidea, which have that structure. Late in the Famennian the Theodossioidea gave rise to several genera assigned to the Ulbospiriferidae, with an inner prismatic shell layer such as is found commonly in various Carboniferous and Permian spiriferids. Late the in Devonian the theodossioids, probably an ulbospiriferid, gave rise to several superfamilies that became dominant elements of the Late Paleozoic brachiopod faunas, namely the Spiriferoidea, Paeckelmanelloidea, and Brachythyridoidea.

Soon after the proliferation of the capillate Spiriferidina the Delthyridina appeared as a second major branch of impunctate genera, including *Howellella* and *Delthyris,* and characterized by a fimbriate shell fabric. Remnants of a transitional shell fabric are present in the Silurian and Lower Devonian Cyrtinopsididae and Acrospiriferidae of the Superfamily Delthyridoidea, but by the Middle Devonian the two suborders were well represented and distinct. The Devonian history of the Delthyridina is also one of proliferation and diversity, represented by numerous families and subfamilies. By the Carboniferous most of the delthyridoid families had disappeared, but the reticularioids, which arose from the Delthyridina in the Silurian, flourished with great diversity until the end of the era.

The origin of the Delthyridina is not known. Gourvennec (1989, 1991) has amply demonstrated that the micro-ornament of this group is substantially different from that of the eospiriferids. It is possible that the Delthyridina were derived from a group other than the eospiriferids or from a common ancestor, in which case the Spiriferida, as presented here, is diphyletic.

Two additional superfamilies, the Ambocoelioidea and the Martinioidea, split off from the Spiriferidina in the Silurian. There has been uncertainty about the derivation of these two superfamilies in the past. The ambocoeliids were judged by Pitrat (1965) to have been derived from an eospiriferid ancestor, but this was disputed by Ivanova (1972) who regarded both the Ambocoelioidea and Martinioidea as having separated from the Delthyridina. Here, we follow Pitrat and also Johnson and Lenz (1992) in regarding the ambocoelioids as having originated from an eospiriferoid stock. We argue here for a similar derivation of the martinioids on the basis of shell fabric and internal morphology of early genera. Ambocoelioid genera are common and diverse in the Devonian, but were reduced to less than a dozen genera in the Late Paleozoic. The martinioids are much less diverse and sporadically represented in the Devonian, but became numerous and diversified in the Carboniferous and Permian, just before their extinction in the Late Permian.

Stratigraphic Range.—Upper Ordovician–Upper Permian.

Suborder Spiriferidina Waagen, 1883
[*nom. correct.* Pitrat, 1965, p. H668
(*pro* suborder Spiriferacea Waagen, 1883, p. 447)]
[*emend.* Carter, Johnson, and Gourvennec, herein]

Diagnosis.—Lateral slopes plicate or costate; fold and sulcus commonly well developed; fine ornament, if present, capillate, pustulose, or imbricate; spinose ornament absent; ctenophoridium absent in early forms.

Stratigraphic Range.—Upper Ordovician–Upper Permian.

Superfamily Cyrtioidea Frederiks, 1924
[*nom. correct.* Johnson, Gourvennec, and Hou, herein
(pro superfamily Cyrtiacea Pitrat, 1965, p. H668);
nom. transl. Pitrat, 1965, (*ex* Cyrtiinae Frederiks, 1924, p. 312)]

Diagnosis.—Biconvex, commonly with fold and sulcus, smooth or plicate; ornament of nonspinose capillae crossed by variably nodose growth lines; deltidium, delthyrial plate, or stegidial plates may be present; dental plates present; crural plates well developed, rudimentary, or lacking.

Stratigraphic Range.—Upper Ordovician (Middle Ashgill)–Lower Devonian (Emsian).

Family Cyrtiidae Frederiks, 1924
[*nom. transl.* Ivanova, 1959, p. 55 (ex Cyrtiinae Frederiks, 1924, p. 312)]
[=Eospiriferinae Schuchert, 1929, p. 20]

Diagnosis.—Delthyrial plate and stegidial plates lacking; crural plates commonly well developed.

Stratigraphic Range.—Upper Ordovician (Middle Ashgill)–Lower Devonian (Emsian).

Subfamily Cyrtiinae Frederiks, 1924
[Cyrtiinae Frederiks, 1924, p. 312]

Diagnosis.—Ventribiconvex, ventral valve hemipyramidal, with catacline or procline interarea, narrowly elongate delthyrium; deltidium with medial foramen; ctenophoridium absent.

Discussion.—The species *Cyrtia approximans* (Barrande, 1879) was listed as Devonian Ff2 by Barrande (1879) and from the Acanthopyge Limestone by Havlíček, (1959:75). This led Boucot (1963) to list the upper range of *Cyrtia* as lower Devonian, but other Devonian occurrences of *Cyrtia* have not been verified. A query to Havlíček brought the following response (written communication, July 11, 1991): "*Cyrtia approximans* (Barrande) is a true *Cyrtia*! The data about its age and type locality, however, are not correct in Barrande's paper. After revising this species, I came to the conclusion that *Cyrtia approximans* is conspecific with the Silurian *Cyrtia spiriferoides* Bouček, 1941 (Wenlock, Motol Formation)."

Stratigraphic Range.—Upper Silurian (Upper Wenlockian–Ludlovian).

Genera Included.—*Cyrtia* Dalman, 1828; *Plicocyrtia* Boucot, 1863; *Dongbeiispirifer* Liu, 1977.

Subfamily Eospiriferinae Schuchert, 1929
[Eospiriferinae Schuchert in Schuchert and Levene, 1929, p. 20]

Diagnosis.—Biconvex with curved, commonly apsacline ventral interarea and open delthyrium; deltidium present; ctenophoridium commonly absent.

Discussion.—In the list below of assigned genera we retain *Macropleura* although it was regarded as a junior subjective synonym of *Hedeina* after the type species of *Hedeina* was made known by Brunton et al. (1967). Boucot (1975:362) suggested retaining *Macropleura* for large-sized Lower Devonian species, but we propose to include both large and small species based on the amplitude of plications and interspaces rather than on shell size. *Macropleura* has a few prominent plications and deep, U-shaped interspaces. *Hedeina* is characterized by broad, low plications and shallow interspaces. Probably, *Hedeina* was derived from *Eospirifer* and belongs to a different branch of eospiriferid phylogeny than *Macropleura.* Our definition would include *Hedeina ananias* Johnson, Boucot, and Murphy (1976) in *Macropleura.* We also synonymize *Ejnespirifer* Fu, 1982 with *Macropleura* on the same basis. According to Rong Jia-yu (written communication, March 6, 1994) the type species of *Ejnespirifer* does not have strut-like accessory plates in the dorsal valve as were illustrated by Fu (1982:177, fig. 92B).

Stratigraphic Range.—Upper Ordovician (Middle Ashgill)–Lower Devonian (Emsian).

Genera Included.—*Eospirifer* Schuchert, 1913; *Badainjarania* Zhang, 1981; *Endospirifer* Tachibana, 1981; *Espella* Nilova, 1965 [=*Laevispirifer* Ushatinskaia, 1977]; *Havlicekia* Boucot, 1963; *Hedeina* Boucot, 1957; *Janius* Havlíček, 1957; *Lobvia* Breivel and Breivel, 1977; *Macropleura* Boucot, 1963 [=*Ejnespirifer* Fu, 1982]; *Mictospirifer* Johnson, 1995; *Myriospirifer* Havlíček, 1978 [=*Acutilineolus* Amsden, 1978]; *Nurataella* Larin, 1973 [=*Baterospirifer* Rong, Su, and Li, 1984]; *Striispirifer* Cooper and Muir-Wood, 1951; *Yingwuspirifer* Rong, Xu, and Yang, 1974; *Xinanospirifer* Rong, Xu, and Yang, 1974.

Family Hedeinopsidae Gourvennec, 1990
[*nom. transl.* Johnson, herein
(*ex* Hedeinopsinae Gourvennec, 1990, p. 142)]

Diagnosis.—Plicate, ventribiconvex, with stegidial plates and delthyrial plate; crural plates rudimentary or absent; ctenophoridium present.

Stratigraphic Range.—Upper Silurian (Wenlockian–Pridolian).

Subfamily Hedeinopsinae Gourvennec, 1990
[Hedeinopsinae Gourvennec, 1990, p. 142]

Diagnosis.—As for the family.

Discussion.—Examination of the holotype of *Tannuspirifer dixoni* Jones (1980: pl. 1, fig. 1), on loan from Jones, reveals that it has stegidial plates.

Stratigraphic Range.—Upper Silurian (Wenlockian–Pridolian).

Genera Included.—*Hedeinopsis* Gourvennec, 1990; *Tannuspirifer* Ivanova, 1960.

Superfamily Spinelloidea Johnson, 1970
[*nom. transl.* Johnson and Hou, herein
(*ex* Spinnellinae Johnson, 1970, p. 205)]

Diagnosis.—Biconvex, with fold and sulcus; plicate; ornament nonfrilly, capillate; delthyrial plate lacking; dental plates, without median septum.

Stratigraphic Range.—Upper Silurian (Wenlockian)–Upper Devonian (Upper Famennian).

Family Spinellidae Johnson, 1970
[*nom. transl.* Wang and Rong, 1986, p. 200
(*ex* Spinellinae Johnson, 1970, p. 205)]

Diagnosis.—Multiplicate, with smooth or medially grooved fold and smooth or medially plicate sulcus.

Stratigraphic Range.—Upper Silurian (Wenlockian)–Upper Devonian (Upper Famennian).

Subfamily Spinellinae Johnson, 1970
[Spinellinae Johnson, 1970, p. 205]
[=Guerichellinae Paeckelmann, 1931, p. 24]

Diagnosis.—Multiplicate, with smooth fold and sulcus, or with medial plication in sulcus; crural plates short or lacking.

Stratigraphic Range.—Lower Devonian (Pragian)–Upper Devonian (Upper Famennian).

Genera Included.—*Spinella* Talent, 1956; *Acutatheca* Stainbrook, 1945; *Adolfia* Gürich, 1909 [=*Guerichella* Paeckelmann, 1913; =*Changshaispirifer* Zhao, 1977]; *Allanella* Crickmay, 1953 [=*Minutilla* Crickmay, 1967]; *Chimaerothyris* Paulus, Struve, and Wolfart, 1963; *Eospiriferina* Grabau, 1931; *Fidespirifer* Liashenko, 1973; *Guicyrtia* Wang and Zhu, 1979; *Volgospirifer* Shevchenko, 1970.

Subfamily Pinguispiriferinae Havlíček, 1971
[Pinguispiriferinae Havlíček, 1971, p. 27]

Diagnosis.—Plicate, with weak to obscure capillae, crossed by fila; crural plates short or lacking.

Discussion.—Several genera of the Pinguispiriferinae have been classified with the eospiriferids in the past, but although capillate they lack the well-developed capillae typical of eospiriferids. Others differ also in the construction of the cardinalia. *Nikiforovaena* Boucot, 1963, previously unknown in the dorsal interior, was examined by preparing a dorsal internal mold of the type species; it revealed the presence of a ctenophoridium and short, divergent crural plates.

Stratigraphic Range.—Upper Silurian (Wenlockian)–Middle Devonian (Eifelian).

Genera Included.—*Pinguispirifer* Havlíček, 1957; *Amoenospirifer* Havlíček, 1957; *Brevispirifer* Cooper, 1942; *Ljudmilispirifer* Cherkesova, 1976; *Nikiforovaena* Boucot, 1963; *Spurispirifer* Havlíček, 1971.

Subfamily Callispiriferinae Johnson, **new subfamily**

Diagnosis.—Non-capillate, with high flat ventral interarea.

Stratigraphic Range.—Lower Devonian (Emsian).

Genera Included.—*Callispirifer* Perry, 1984; *Rochtex* Havlíček, 1990.

Subfamily Eurekaspiriferinae Johnson, **new subfamily**

Diagnosis.—Capillate, with dorsal adminicula.

Discussion.—The presence of dorsal adminicula in *Eurekaspirifer* suggests an even greater separate ranking than subfamily, but as no closely related genera are now known proposal of a more substantial taxonomy seems inappropriate.

Stratigraphic Range.—Lower Devonian (Lower Emsian).

Genera Included.—*Eurekaspirifer* Johnson, 1966.

Family Echinospiriferidae Liashenko, 1973
[Echinospiriferidae Liashenko, 1973, p. 109]
[=Rigauxidae Brice, 1988, p. 371]

Diagnosis.—Multiplicate, with plicate fold and sulcus.

Discussion.—A specimen of the type species of *Arctospirifer* Stainbrook, 1950 was sectioned confirming the absence of a delthyrial plate and the absence of crural plates. *Regauxia* Brice, 1988 includes the widely represented North American species *Spirifer orestes* Hall and Whitfield and *Spirifer strigosus* Meek, both of which have been assigned mistakenly to *Indospirifer* Grabau, 1931 by various authors.

Stratigraphic Range.—Lower Devonian (Pragian)–Upper Devonian (Upper Famennian).

Genera Included.—*Echinospirifer* Liashenko, 1973; *Adolfispirifer* Krylova, 1962; *Arctospirifer* Stainbrook, 1950; *Enchondrospirifer* Brice, 1971; *Hispidaria* Cooper and Dutro, 1982; *Howittia* Talent, 1956 [=*Glyptospirifer* Hou and Xian, 1975]; *Indospirifer* Grabau, 1931 [=*Schizospirifer* Grabau, 1931]; *Regauxia* Brice, 1988; *Sergunkovia* Nalivkin, 1979.

Superfamily Theodossioidea Ivanova, 1959
[*nom. transl.* Johnson, Carter, and Hou, herein
(*ex* Theodossiinae Ivanova, 1959, p. 61)]

Diagnosis.—Uniformly plicate or costate, with fold and sulcus indistinct or lacking; delthyrial plate lacking.

Discussion.—The superfamily Theodossioidea, with its one new family and three new subfamilies, unites genera that are plicate or costate over the entire exterior and which lack a well-defined fold and sulcus. An implication in this classification is that there are genetic links from the earliest genera of the subfamily Branikiinae, of Emsian age, to the Middle Devonian genera of the Theodossiinae. However, the origin of the Branikiinae is uncertain. The genus *Theodossia* is the supposed link to Famennian and younger genera of the Ulbospiriferidae, which are characterized by the presence of an inner prismatic shell layer. The Early and Middle Devonian genera are uncommon taxa and this together with their unusual morphology has resulted in their previously being outside of generally accepted spiriferid systematics.

Stratigraphic Range.—Lower Devonian (Pragian)–Upper Devonian (Upper Famennian).

Family Theodossiidae Ivanova, 1959
[*nom. transl.* Johnson, Carter, and Hou, herein
(*ex* Theodossiinae Ivanova, 1959, p. 61)]

Diagnosis.—Without inner prismatic shell layer.

Stratigraphic Range.—Lower Devonian (Pragian)–Upper Devonian (Frasnian).

Subfamily Theodossiinae Ivanova, 1959
(Theodossiinae Ivanova, 1959, p. 61)

Diagnosis.—Capillate.

Stratigraphic Range.—Middle Devonian (Eifelian)–Upper Devonian (Frasnian).

Genera Included.—*Theodossia* Nalivkin, 1925 [=*Vandergrachtella* Crickmay, 1953]; *Paralazutkinia* Jiang, 1978 [=*Pinghuangella* Jiang, 1978]; *Urella* Rzhonsnitskaia, 1960 [=*Retzispirifer* Kulkov, 1960].

Subfamily Branikiinae Johnson and Hou, **new subfamily**

Diagnosis.—Noncapillate.
Stratigraphic Range.—Lower Devonian (Pragian)–Middle Devonian (Eifelian).
Genera Included.—*Branikia* Havlíček, 1957 [=*Bidentatus* Khodalevich and Breivel, 1972]; *Jilinospirifer* Su, 1980; *Lenzia* Perry, Boucot, and Gabrielse, 1981.

Family Ulbospiriferidae Johnson and Carter, **new family**

Diagnosis.—With inner prismatic shell layer.
Stratigraphic Range.—Upper Devonian (Upper Famennian).

Subfamily Ulbospiriferinae Johnson and Carter, **new subfamily**

Diagnosis.—Uniformly costate.
Stratigraphic Range.—Upper Devonian (Upper Famennian).
Genera Included.—*Ulbospirifer* Grechishnikova, 1965; *Cyrtiorina* Cooper and Dutro, 1982; *Tenisia* Martynova, 1970 [=*Omolonospirifer* Simakov, 1970].

Subfamily Palaeospiriferinae Carter, Johnson, and Hou, **new subfamily**

Diagnosis.—With low, rounded plications.
Stratigraphic Range.—Upper Devonian (Upper Famennian).
Genera Included.—*Palaeospirifer* Martynova and Sverbilova, 1968 [=*Goungjunspirifer* Zhang, 1983].

Family Palaeochoristitidae Carter, **new family**

Diagnosis.—Cardinal extremities rounded in juveniles, outline variable in adults; well-developed dental adminicula and dorsal adminicula present; micro-ornament absent.
Discussion.—The origins of this family are obscure because dorsal adminicula are rare in the Theodossioidea. The only known Devonian theodossioid genus with dorsal adminicula is the Russian Middle Devonian genus *Urella* Rzhonsnitskaya, 1960, which is presumed to be in the line of ancestry of the palaeochoristitids.
Stratigraphic Range.—Lower Carboniferous (Tournaisian).
Genera Included.—*Palaeochoristites* Sokolskaya, 1941; *Eochoristites* Chu, 1933 [=*Centrospirifer* Tien, 1938].

Superfamily Cyrtospiriferoidea Termier and Termier, 1949
[*nom. transl.* Ivanova, 1972, p. 31
(*ex* Cyrtospiriferinae Termier and Termier, 1949, p. 99)]

Diagnosis.—Nonfrilly, capillate or pustulose; delthyrial plate present; ctenophoridium without crural plates.
Stratigraphic Range.—Lower Devonian (Emsian)–Upper Devonian (Upper Famennian).

Family Spinocyrtiidae Ivanova, 1959
[*nom. transl.* Pitrat, 1965, p. H688
(*ex* Spinocyrtiinae Struve, 1963, p. 462,
nom. correct. pro Spinocyrtinae Ivanova, 1959, p. 59)]

Diagnosis.—Multiplicate, with smooth or medially grooved fold and smooth or medially plicate sulcus.
Stratigraphic Range.—Lower Devonian (Emsian)–Upper Devonian (Frasnian).
Genera Included.—*Acutoria* Cooper and Dutro, 1982; *Alatiformia* Struve, 1963;

Eosyringothyris Stainbrook, 1943; *Mediospirifer* Bublitchenko, 1956 [=*Carpinaria* Struve, 1982]; *Duryeella* Boucot, 1975; *Orthospirifer* Pitrat, 1975; *Platyrachella* Fenton and Fenton, 1924; *Spinocyrtia* Frederiks, 1916; *Subcuspidella* Mittmeyer, 1965 [=*Tenuicostella* Mittmeyer and Geib, 1967].

Family Cyrtospiriferidae Termier and Termier, 1949
[*nom. transl.* Beznosova, 1958, p. 17
(*ex* Cyrtospiriferinae Termier and Termier, 1949, p. 99)]

Diagnosis.—Nonfrilly, flanks costate; fold and sulcus finely costate.

Discussion.—The assignments of at least 19 genera to one of two subfamilies on the basis of shell shape is inadequate. A re-evaluation of the genera of the Family Cyrtospiriferidae on the basis of internal structures is obviously needed. An initial appraisal might usefully involve a determination of dental plates (intrasinal or extrasinal).

Stratigraphic Range.—Middle Devonian (Upper Givetian)–Upper Devonian (Upper Famennian).

Subfamily Cyrtospiriferinae Termier and Termier, 1949
[Cyrtospiriferinae Termier and Termier, 1949, p. 99]
[=Hunanospiriferinae Beznosova, 1958, p. 17]

Diagnosis.—Wide interarea with acute cardinal angles.

Stratigraphic Range.—Upper Devonian (Frasnian–Upper Famennian).

Genera Included.—*Cyrtospirifer* Nalivkin in Frederiks, 1924 [=*Hunanospirifer* Tien, 1938; *Grabauispirifer* Gatinaud, 1949; *Eurytatospirifer* Gatinaud, 1949; *Deothossia* Gatinaud, 1949; *Lamarckispirifer* Gatinaud, 1949; *Subquadriangulispirifer* Sartenaer, 1982]; *Austrospirifer* Glenister, 1956; *Geminisulcispirifer* Sartenaer, 1982; *Liraspirifer* Stainbrook, 1950; *Petshorospirifer* Fotieva, 1985; *Regelia* Crickmay, 1952; *Sinospirifer* Grabau, 1931; *Sphenospira* Cooper, 1954; *Syringospira* Kindle, 1909; *Tarandrospirifer* Simakov, 1970; *Tenticospirifer* Tien, 1938 [=*Conispirifer* Liashenko, 1985].

Subfamily Cyrtiopsinae Ivanova, 1972
[Cyrtiopsinae Ivanova, 1972, p. 33]
[=?Uchtospiriferidae Liashenko, 1973, p. 87]

Diagnosis.—Narrow interarea with rounded cardinal angles.

Discussion.—*Cyrtiopsis* Grabau has been widely reported in Famennian rocks, but lack of knowledge of the *Cyrtiopsis* interior, as well as lack of critical attention to shell form makes many citations of the genus dubious. Examples are in the influential paper by Crickmay (1952), including taxa he named *Cyrtiopsis nahanniensis* and *C. normandvillana.* We cite these two taxa because Crickmay provided drawings intended to represent the disposition of the dental plates as intrasinal and recurved distally (1952:pl. 72, fig. 12; pl. 74; fig. 4). We have examined specimens of these two species in the Crickmay collections, on loan from the Paleontological Research Institution, Ithaca, New York. Dental lamellae observed in internal molds of both species are intrasinal, but long and straight rather than being recurved distally. In this they resemble a prepared internal mold in our possession of the type species *C. davidsoni,* but they differ from it in shell form. *Cyrtiopsis davidsoni* has a deep, wide, and sharply bounded ventral sulcus that gives it a distinctive shell shape. We know of no North American species like it.

Stratigraphic Range.—Middle Devonian (Upper Givetian)–Upper Devonian (Famennian).

Genera Included.—*Cyrtiopsis* Grabau, 1923 [=*Grabauicyrtiopsis* Gatinaud, 1949; *Sinocyrtiopsis* Gatinaud, 1949]; *Dichospirifer* Brice, 1971; *Dmitria* Sidiachenko, 1961; *Eodmitria* Brice, 1982; *Platyspirifer* Grabau, 1931; *Uchtospirifer* Liashenko, 1957 [=*Timanospirifer, Nordispirifer,* and *Clivospirifer* Liashenko, 1973]; *Mennespirifer* Liashenko, 1973 [=*Komispirifer* Liashenko, 1973]; *Acutella* Liashenko, 1973.

Superfamily Ambocoelioidea George, 1931
[*nom. transl.* Johnson and Carter, herein
(*ex* Ambocoeliinae George, 1931, p. 42]

Diagnosis.—Commonly small, lacking well-developed fold and sulcus; cardinal process commonly simple, knoblike; outer hinge plates broad, well developed; cruralium variably developed.

Stratigraphic Range.—Upper Silurian (Upper Wenlockian)–Permian.

Family Ambocoeliidae George, 1931
[*nom. transl.* Ivanova, 1959, p. 56
(*ex* Ambocoeliinae George, 1931, p. 42)]

Diagnosis.—Ventribiconvex, smooth shells, rarely pauciplicate; commonly lacking dental plates.

Stratigraphic Range.—Upper Silurian (Upper Wenlockian)–Permian.

Subfamily Ambocoeliinae George, 1931
[Ambocoeliinae George, 1931, p. 42]

Diagnosis.—Crural plates vestigial or lacking; commonly with fine concentric growth lamellae, and fine capillae on older genera; dental plates lacking in younger genera.

Discussion.—Pitrat (1965:H667) suggested that the ambocoeliid brachiopods were derived from the Eospiriferinae, based on age of appearance, nonstriate site of dorsal diductor attachment, crural plates, and permissive similarities of fine ornament. Although Pitrat erred in attributing crural plates to the earliest ambocoeliids, the derivation seems plausible, beginning with the oldest ambocoeliid *Eoplicoplasia* Johnson and Lenz, 1992. *Eoplicoplasia* morphology suggests derivation from a plicate eospiriferid genus such as *Macropleura* Boucot. This is based on the presence of *Macropleura* in older Silurian beds (Boucot, 1963:706; Havlíček, 1980:11), similar overall shell shape, nonstriate site of dorsal diductor attachment, dental plates, and the presence on *Eoplicoplasia* of a relict eospiriferid radial ornament of fine capillae (Lenz, 1972:pl. 2, fig. 2, 21). *Eoplicoplasia* and *Plicoplasia* both lack crural plates, consistent with their assignment to the Subfamily Ambocoeliinae (Johnson and Trojan, 1982:128–129).

Stratigraphic Range.—Upper Silurian (Upper Wenlockian)–Permian.

Genera Included.—*Ambocoelia* Hall, 1860; *Attenuatella* Stehli, 1954; *Aviformia* Xian, 1988; *Biconvexiella* Waterhouse, 1983; *Bisinocoelia* Havlíček, 1953; *Cruricella* Grant, 1976; *Crurithyris* George, 1931; *Cyrtinoides* Iudina and Rzhonsnitskaia, 1985 [=*Mucroclipeus* Goldman and Mitchell, 1990]; *Dicoelospirifer* Zhang, 1989; *Echinocoelia* Cooper and Williams, 1935 [=*Pyramina* Liashenko, 1969]; *Eoplicoplasia* Johnson and Lenz, 1992; *Guangxiispirifer* Xian, 1983; *Orbicoelia* Waterhouse and Piyasin, 1970; *Paracrurithyris* Liao, 1979; *Plicoplasia* Boucot,

1959; *Metaplasia* Hall and Clarke, 1893; *Spinoplasia* Boucot, 1959; *Swaicoelia* Hamada, 1968.

Subfamily Rhynchospiriferinae Paulus, 1957
[Rhynchospiriferinae Paulus, 1957, p. 51]
[=Ilmeniinae Dürkoop, 1970, p. 195]

Diagnosis.—Crural plates well developed, either discrete or joined to form a cruralium; commonly with fine capillae; dental plates present or absent.

Stratigraphic Range.—Lower Devonian (Emsian)–Upper Devonian (Frasnian).

Genera Included.—*Amboglossa* Wang and Zhu, 1979; *Ambothyris* George, 1931; *Changtangella* Xian, 1982; *Choperella* Liashenko, 1969; *Crurispina* Goldman and Mitchell, 1990; *Diazoma* Dürkoop, 1970 [=*Kelusia* Mamedov, 1978]; *Emanuella* Grabau, 1923; [=*Paraemanuella* Yang, 1977]; *Ilmenia* Nalivkin, 1941; *Ilmeniopsis* Xian, 1982; *Ilmenispina* Havlícek, 1959; *Ilmospirifer* Liashenko, 1969; *Ladjia* Veevers, 1959; *Levibiseptum* Xian, 1975; *Moravilla* Havlícek, 1953; *Rhynchospirifer* Paulus, 1957 [=*Kosirium* Ficner and Havlíček, 1975; *Biarella* Markovski, 1988]; *Zhonghuacoelia* Chen, 1978.

Family Verneuiliidae Schuchert, 1929
[*nom. transl.* Brunton, 1984, p. 101
(*ex* Verneuiliinae Schuchert, 1929, p. 21)]

Diagnosis.—Transverse to subcircular, biconvex, with opposite folding forming ligate to metacarinate anterior margins; ventral interarea narrow to full width of valves, with open delthyrium or restricted by apical deltidium; growth lines without capillae.

Stratigraphic Range.—Middle Devonian (Eifelian)–Lower Carboniferous.

Genera Included.—*Verneuilia* Hall and Clarke, 1893; *Minythyra* Brunton, 1984; *Nuguschella* Tiazheva, 1960.

Family Lazutkiniidae Johnson and Hou, **new family**

Diagnosis.—Wholly plicate, lacking capillae; with dental plates.

Stratigraphic Range.—Lower Devonian (Emsian)–Middle Devonian (Givetian).

Genera Included.—*Lazutkinia* Rzhonsnitskaia, 1952 [=*Yavorskiella* Lazutkin in Yavorsky, 1940]; *Prolazutkinia* Hou and Xian, 1983.

Family Eudoxinidae Nalivkin, 1979
[*nom. correct. et transl.* Carter, herein
(*pro* Subfamily Eudoxininae Nalivkin, 1979, p. 145)]

Diagnosis.—Small to very large; biconvex; costate or costellate; micro-ornament papillose in some, absent or unknown in most genera; dental adminicula and protuberant ctenophoridium absent.

Discussion.—The lack of a convex ctenophoridium in this group convincingly points to its derivation from the eospiriferid–ambocoeliid lineage. There is a great difference in size between the Early Carboniferous *Eudoxina* and *Paulonia* and the Permian *Costicrura* and *Wilberrya.* In the absence of intermediate forms of Visean or Upper Carboniferous age the homogeneity of this group cannot be tested easily.

Stratigraphic Range.—Upper Devonian (Famennian)–Upper Permian.

Genera Included.—*Eudoxina* Frederiks and Kruglov, 1928; *Costicrura* Hoover, 1981; *Paulonia* Nalivkin, 1925; *Wilberrya* Yancey, 1978.

Superfamily Martinioidea Waagen, 1883
[*nom. correct.* Carter, Johnson, and Gourvennec, herein
(*pro* Martiniacea Waagen, 1883;
nom. transl. Ivanova, 1972, p. 41,
ex Subfamily Martiniinae Waagen, 1883, p. 524)]

Diagnosis.—Biconvex, with broadly rounded lateral extremities and short hingeline; lateral slopes smooth or with subdued ribbing; micro-ornament commonly capillate, smooth, or very finely spinulose, but not strongly lamellose or concentrically disposed; ventral median septum absent; dorsal interior with ctenophoridium in all but the earliest genera, commonly with crural plates or dorsal adminicula; surface commonly pitted.

Discussion.—This superfamily is now believed to have been derived from the ambocoeliids in Late Silurian time through the acquisition of consistently inflated dorsal valves and pitted micro-ornament. The earliest family, the Tenellodermidae, lack a ctenophoridium, attesting to their derivation from the ambocoelioids. Internally, the appearance of crural plates or strong dorsal adminicula is manifested in several lineages throughout most of the history of the superfamily.

Stratigraphic Range.—Silurian (Upper Wenlock)–Upper Permian.

Family Tenellodermidae Carter, Johnson, and Gourvennec, **new family**

Diagnosis.—Ctenophoridium absent; surface pitted or simple; dental plates present.

Discussion.—In the absence of a ctenophoridium these two genera provide a convincing transition from the ambocoelioids to ctenophoridium-bearing Late Paleozoic martinioids. The earliest species of both genera occur in the Upper Wenlockian of Bohemia, but we suggest that *Tenellodermis* most closely resembles an ambocoeliid ancester in its simple cardinalia having neither striate cardinal process nor crural plates.

Stratigraphic Range.—Silurian (Upper Wenlockian)–Middle Devonian (Eifelian).

Genera Included.—*Cingulodermis* Havlíček, 1971; *Tenellodermis* Havlíček, 1971.

Family Elythynidae Gourvennec, **new family**

Diagnosis.—Flanks plicate; ornament of fine pits or spines and pits; ctenophoridium, dental plates, and crural plates or dorsal adminicula present.

Discussion.—These genera are unified by their similar internal morphology and represent the earliest martinioids with a ctenophoridium. Externally, they vary in their micro-ornament.

Elythyna has fine elongate pits or grooves arranged in quincunx similar to the Ingelarellidae. Examination of topotype material of the type species, *E. salarica,* shows that there are short subparallel crural plates (or dorsal adminicula?) and a ctenophoridium. *Najadospirifer* Havlíček possesses discontinuous capillae with fine ovate pits radially arranged in the interspaces (Havlíček, 1971:pl. 1, 2) and internally the crural plates are very short (Boucot, 1962:pl. 49). *Tatjanaspirifer* is assigned here despite its ornament of radial marginal spinules of the reticularioid type. This genus also shows randomly distributed pits which were originally

diagnosed as coarse spine bases by Cherkesova. This pitted ornament is unknown in the reticularioids and strongly suggests affinity with the martinioids. These pits are sometimes best seen in the fibrous layer and may not be apparent unless the outer layer is exfoliated, a feature common in the martinioids.

Stratigraphic Range.—Lower Devonian (Pragian)–Middle Devonian (Givetian).

Genera Included.—*Elythyna* Rzhonsnitskaya, 1952; *Najadospirifer* Havlíček, 1957; *Tatjanaspirifer* Cherkesova, 1991.

Family Martiniidae Waagen, 1883
[*nom. transl.* Ivanova, 1959, p. 56,
ex Subfamily Martiniinae Waagen, 1883, p. 524]

Diagnosis.—Ctenophoridium present; subequally biconvex; lateral slopes smooth or weakly plicate; crural plates or dorsal adminicula absent; micro-ornament of scattered surficial pits, and/or capillae, or absent.

Stratigraphic Range.—Upper Devonian (Famennian)–Upper Permian.

Subfamily Martiniinae Waagen, 1883
[Subfamily Martiniinae Waagen, 1883, p. 524]

Diagnosis.—Lacking plates or septa in either valve; micro-ornament of fine pits only.

Stratigraphic Range.—Lower Carboniferous–Upper Permian.

Genera Included.—*Martinia* McCoy, 1844 [=*Jilinmartinia* Lee and Gu, 1980; *Paramartinia* Reed, 1949; *Pseudomartinia* Leidhold, 1928]; *Beschevella* Poletaev, 1975; *Implexina* Poletaev, 1971; *Kalitvella* Lazarev and Poletaev, 1982; *Postamartinia* Want and Yang, 1993; *Spinomartinia* Waterhouse, 1968; *Tiramnia* Grunt, 1977; *Weiningia* Ching and Liao, 1974 [=*Elenchus* Aleksandrov, 1973].

Subfamily Eomartiniopsinae Carter, **new subfamily**

Diagnosis.—Dental adminicula present; lateral slopes commonly weakly ribbed; micro-ornament of fine pits or absent.

Discussion.—The genus *Eomartiniopsis* Sokolskaya has been repeatedly reported in Devonian strata but we have doubts about the validity of these reports. A detailed investigation of the dorsal interiors and micro-ornament of these species is necessary to resolve this problem. The type species lacks crural plates or dorsal adminicula. If we assume that all of the species, including Devonian ones, assigned here by Sokolskaia (1941) also lack crural plates, the number of Devonian species in need of future investigation is much reduced.

Five species were assigned to this genus by Rzhonsnitskaia (1952), but she did not provide morphological evidence for her assignment. One of them, *Spirifer kirki,* undoubtedly belongs to *Warrenella.* The same might be said for *Spirifer laevis* judging from the presence of a pseudodeltidium, strong apical callosity, deep muscle scars, etc. *Spirifer maia* was probably assigned here based on external aspect, for no information is available concerning its internal structure. Apparently *S. maia* possesses a pseudodeltidium which would suggest relationship to *Warrenella,* but more information is needed to confirm this assignment. The dorsal

interiors of *Eomartiniopsis lazutkini* and *Spirifer linguifer* have never been described.

Havlícek (1959) assigned six more Devonian species and subspecies to *Eomartiniopsis.* He later 1971) restricted his concept of the genus to include only Carboniferous species and assigned his previous species to his genera *Tenellodermis* and *Cingulodermis.* However, several Devonian species cannot be assigned to these genera. Among them, *E. sellata* [*Spirifer* (*Martinia*) *inflata sellata* Paeckelmann, 1913] is assigned here, but its dorsal interior is poorly known. The ornament of *Eomartiniopsis lazutkini* and *Spirifer linguifer,* both Eifelian and mentioned above, consists of quincuntially arranged pits, an ornament unknown in *Cingulodermis,* but which evokes the Ingellarellidae. On the other hand the described ornament of *Cingulodermis* may be an artifact of preservation and incompletely known, for it is seemingly within the lineage of *Tenellodermis* (its ancestor) and *Eomartiniopsis* (its presumed descendant), both of which possess pits.

The last Devonian species assigned to *Eomartiniopsis* is *E. zeravschanica,* a *nomen nudum,* and is very poorly known. Thus, the presence of *Eomartiniopsis* in the Devonian cannot be ascertained. It has been treated as a "grab-bag" genus for smooth, poorly described reticularioids occurring in Devonian strata. Further investigation will probably show that most Devonian species of "*Eomartiniopsis*" would be better assigned to *Cingulodermis, Warrenella,* or similar genera.

Stratigraphic Range.—?Devonian, Lower Carboniferous–Upper Permian.

Genera Included.—*Eomartiniopsis* Sokolskaya, 1941; *Globispirifer* Tachibana, 1964; *Heteraria* Cooper and Grant, 1976; *Kisilia* Nalivkin, 1979; *Merospirifer* Reed, 1949; *Rallacosta* Cooper and Grant, 1976.

Subfamily Elivellinae Carter, **new subfamily**

Diagnosis.—Micro-ornament of capillae and fine pits; dental plates becoming progressively shorter in younger genera.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Lower Permian.

Genera Included.—*Elivella* Frederiks, 1924; *Martiniella* Grabau and Tien, 1931; *Ushkolia* Martynova and Sverbilova, 1969; *Moumina* Frederiks, 1924.

Family Martiniopsidae Kotljar and Popeko, 1967
[*nom. transl.* Carter, herein,
ex Martiniopsinae Kotljar and Popeko, 1967, p. 182]

Diagnosis.—Dental and crural plates or dorsal adminicula present; lateral slopes commonly with weak plications; micro-ornament usually weakly to strongly capillate.

Stratigraphic Range.—Lower Carboniferous (Tournaisian)–Upper Permian.

Genera Included.—*Martiniopsis* Waagen, 1883 [=*Rorespirifer* Waterhouse and Piasin, 1970]; *Arktikina* Grunt, 1977; *Crassumbo* Carter, 1967; *Nodaea* Tachibana, 1981.

Family Ingelarellidae Campbell, 1959
[*nom. transl.* Archbold and Thomas, 1986, p. 582,
ex Ingelarellinae Campbell, 1959, p. 333]

Diagnosis.—Micro-ornament of quincuncially arranged elongate grooves and ridges; ventral interior with dental adminicula.

Discussion.—The genera in this family are differentiated and assigned to subfamilies on the basis of micro-ornament, the nature of which is poorly known for

several genera. Reassignment or synonymizing of one or more genera is likely to be necessary.

Stratigraphic Range.—Lower Carboniferous (Visean)–Upper Permian.

Subfamily Ingelarellinae Campbell, 1959
[Subfamily Ingelarellinae Campbell, 1959, p. 333]

Diagnosis.—Spinules absent; dorsal adminicula well developed.

Discussion.—*Ambikella* Sahni and Srivastava is based on a single, poorly preserved specimen and its validity has not been confirmed.

Stratigraphic Range.—Lower Carboniferous (Visean)–Upper Permian.

Genera Included.—*Ingelarella* Campbell, 1959; *?Ambikella* Sahni and Srivastava, 1956; *Fredericksia* Paeckelmann, 1931; *Tabellina* Waterhouse, 1986; *Tomiopsis* Benediktova, 1956 [=*Danzania* Pavlova, 1989].

Subfamily Notospiriferinae Archbold and Thomas, 1986
[Subfamily Notospiriferinae Archbold and Thomas, 1986, p. 584]

Diagnosis.—Fold and sulcus well developed; micro-ornament of quincuncially arranged grooves and ridges, with anteriorly directed spinules at posterior ends of short grooves, and with deep elongate globose pits extending into secondary layer under spinules; dorsal adminicula short or absent.

Stratigraphic Range.—Upper Carboniferous or Lower Permian–Upper Permian.

Genera Included.—*Notospirifer* Harrington, 1955; *Farmerella* Clarke, 1992.

Subfamily Glendoniinae Clarke, 1992
[Subfamily Glendoniinae Clarke, 1992, p. 75]

Diagnosis.—Micro-ornament of quincuncially arranged shallow elongate grooves terminated anteriorly by low elongate spinules and shallow elongate pits.

Stratigraphic Range.—Permian (Asselian–Kazanian).

Genera Included.—*Glendonia* McClung and Armstrong, 1978; *Birchsella* Clarke, 1987; *Homevalaria* Waterhouse, 1986; *Kelsovia* Clarke, 1990.

Family Gerkispiridae Carter, 1985
[Family Gerkispiridae Carter, 1985, p. 376]

Diagnosis.—Ovate to transverse; lateral slopes costate; hingeline short; fold-sulcus moderately to well developed; delthyrium with low thin flaring stegidial plates; ventral interior with short thin dental adminicula, commonly with low apical myophragm; dorsal interior with short converging crural plates and small ctenophoridium; micro-ornament of quincuncially arranged very fine uniramous hollow spinules or papillae that originate in fibrous layer.

Discussion.—The genus *Spinospirifer* Martynova differs from the other genera assigned here in having a widely hinged growth form, a single row of spine bases along each plica, and a weakly capillate micro-ornament. It is tentatively placed here due to its spinose ornament and impunctate shell substance.

Stratigraphic Range.—Upper Devonian (Lower Famennian)–Lower Carboniferous (Tournaisian).

Genera Included.—*Gerkispira* Carter, 1983; *Acanthospirina* Schuchert and LeVene, 1929; *Oiosia* Cooper and Dutro, 1982; *Punctothyris* Hyde, 1953; *?Spinospirifer* Martynova, 1961.

Family Perissothyrididae Carter, **new family**

Diagnosis.—Subequally biconvex; transversely subovate; low concave interareas present in both valves; fold moderately developed; sulcus weak, shallow, poorly delimited; lateral slopes with weak simple ribbing; micro-ornament absent; delthyrium very wide, partially occluded apically by "pseudodelthyrial plate" (fused dental flanges?); dental adminicula absent; wide dorsally reflexed dental flanges directed medially; large ctenophoridium supported by short median ridge; crural bases medially directed, with ventrally reflexed medial flanges.

Stratigraphic Range.—Lower Carboniferous.

Genera Included.—*Perissothyris* Carter, 1967; *Mongoliopsis* Grunt, 1977.

Superfamily Spiriferoidea King, 1846
[*nom. correct.* Carter, herein
(*pro* Superfamily Spiriferacea King, 1846, p. 28;
nom. transl. Schuchert, 1896, p. 333, *ex* Spiriferidae King, 1846, p. 28)]

Diagnosis.—Ventral beak incurved, ventral interarea low, usually apsacline; hingeline denticulate except in genera with very narrow hingeline; fold and sulcus usually ribbed; ctenophoridium present; prismatic shell layer present in some genera.

Discussion.—Following Ivanova (1981), the impunctate paeckelmanellids are placed in their own superfamily, the Paeckelmanelloidea. In the previous Treatise classification, Pitrat (1965) placed the genera in this superfamily in the punctate superfamilies Syringothrydoidea and Spiriferinoidea. Also, all punctate genera have been removed from the Spiriferoidea and are now included in the Order Spiriferinida.

This superfamily is severely restricted herein to include only families believed to have been derived from a common ancestor in the Late Devonian. Besides the paeckelmanellids the brachythyridids have been removed from the Spiriferoidea. The brachythyridids are believed to have been derived from a Late Devonian theodossiid ancestral stock that diverged from the line that gave rise to the Spiriferoidea and Paeckelmanelloidea. The Paeckelmanelloidea and Spiriferoidea are judged to have arisen from the same indeterminate theodossiid lineage. This hypothetical theodosiid ancestor may have been strophic, at least partially denticulate, capillate or modified capillate, bearing dental adminicula, and carrying the tendency to produce a prismatic shell layer.

Stratigraphic Range.—Upper Devonian (Famennian)–Upper Permian.

Family Spiriferidae King, 1846
[Family Spiriferidae King, 1846, p. 28]

Diagnosis.—Outline variable; hingeline coarsely denticulate except for narrow areas near delthyrium; delthyrial cover weakly developed or absent; lateral slopes and fold-sulcus costate to costellate; micro-ornament capillate; short delthyrial plate variably developed; dorsal adminicula or crural plates not developed; vascular impressions absent or simple.

Discussion.—This family contains two of the earliest appearing members of the Spiriferoidea, the late Famennian genera *Paralellora* Carter, 1974, of the Subfamily Prospirinae, and *Eobrachythyris* Brice 1971, of the Subfamily Sergospiriferinae. *Eobrachythyris* is most similar to the theodossioids in growth form and macro-ornamentation and could be considered to be closest to a hypothetical ancestor for this superfamily. Such a likely theodossioid ancestor might be *Palaeospirifer*

Martynova and Sverlibova, 1968, except that it lacks any indication of a denticulate or partially denticulate hingeline.

Stratigraphic Range.—Upper Devonian (Famennian)–Upper Permian.

Subfamily Spiriferinae King, 1846
[*nom. transl.* Waterhouse, 1968, p. 9,
ex family Spiriferidae King, 1846, p. 28]

Diagnosis.—Cardinal extremities extended in juveniles; outline variable in adults; flanks and fold-sulcus with numerous costae that commonly bifurcate; fold usually poorly delimited; dental adminicula usually developed, and when present, moderately divergent.

Discussion.—The oldest representatives of this subfamily appear in the late Middle Tournaisian. They were probably derived from a prospirin with a tendency for bifurcation of the ribs such as *Paralellora* or *Unispirifer*. The earliest species of the genus *Spirifer, Spirifer gregeri* Weller, 1914, first appears in the Middle Tournaisian of North America. However, wide and narrow hinged species of the genus *Spirifer* appear virtually simultaneously only slightly later in Western Alberta.

Stratigraphic Range.—Lower Carboniferous (Middle Tournaisian)–Upper Permian.

Genera Included.—*Spirifer* (*Spirifer*) Sowerby, 1818; *Spirifer* (*Grandispirifer*) Yang, 1959; *Spirifer* (*Mesochorispira*) Carter, 1992; *Ectochoristites* Campbell, 1957; *Larispirifer* Enokjan and Poletaev, 1986; *Latispirifer* Archbold and Thomas, 1985; *Warsawia* Carter, 1974.

Subfamily Prospirinae Carter, 1974
[Subfamily Prospirinae Carter, 1974, p. 680]

Diagnosis.—Cardinal extremities extended in juveniles; growth form variable in adults; lateral slopes with relatively few, mostly simple costae; median sulcal costa usually simple or bifurcating once; lateral sulcal costae usually simple, not numerous, derived from sulcus-bounding costae; fold clearly delimited from lateral slopes by bounding interspaces; dental adminicula usually well developed; ventral umbonal callus commonly present.

Discussion.—The early growth stages of *Andreaspira* Abramov and Grigor'eva, *Austrochoristites* Roberts, and *Kasakhstania* Beznosova are poorly known. Large juveniles or young adults of these genera are strongly transverse as seen from illustrations of the growth lines of mature adult specimens. In the absence of definitive information concerning their early development, their assignment here is tentative.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Upper Carboniferous (Upper Serpukhovian, ?Moskovian).

Genera Included.—*Prospira* Maxwell, 1954; ?*Andreaspira* Abramov and Grigor'eva, 1986; ?*Austrochoristites* Roberts, 1971; *Finospirifer* Ying, 1979; ?*Kasakhstania* Beznosova, 1968; *Kinghiria* Litvinovich, 1966; *Paralellora* Carter, 1974; *Subspirifer* Shan and Zhao, 1980; *Unispirifer* Campbell, 1957 [=?*Lytha* Frederiks, 1924].

Subfamily Sergospiriferinae Carter, **new subfamily**

Diagnosis.—Cardinal extremities rounded in juveniles; outline variable in adults; lateral slopes with few, simple or bifurcating costae; lateral sulcal costae usually

simple, derived from bounding costae; fold usually well delimited by bounding interspaces; dental adminicula well developed.

Discussion.—The nature of the hingeline and micro-ornament of *Afghanospirifer* Plodowski are poorly known. If it should prove to be nondenticulate, then it might be related to the Palaeochoristididae. The early growth stages of the type species of *Eobrachythyris* Brice are too poorly known to be certain that they are rounded in all stages. If the cardinal extremities of juveniles of this species prove to be extended, this genus should be reassigned to the Prospirinae.

Stratigraphic Range.—?Upper Devonian (Upper Famennian); Lower Carboniferous (Lower Tournaisian)–Upper Carboniferous; ?Permian.

Genera Included.—?*Afghanospirifer* Plodowski, 1968; *Anthracospirifer* Lane, 1963 [=?*Plicatocyrtia* Gauri, 1965]; *Cancellospirifer* Campbell, 1953; ?*Eobrachythyris* Brice, 1970; *Eochoristitella* Qi, 1983; *Sergospirifer* Ivanova, 1952.

Subfamily Purdonellinae Poletaev, 1986
[*nom. nov.* Poletaev, 1986, p. 65
(*pro* Subfamily Munellinae Frederiks, 1924, p. 313)]

Diagnosis.—Outline brachythyridid; hingeline narrow; fold and sulcus moderately to well developed, multicostate, not delineated by discontinuity in ribbing; costae on lateral slopes often flattened, simple or subfasciculate; ventral interior with delthyrial plate and diverging dental adminicula; vascular impressions indistinct.

Discussion.—The multicostate freely bifurcating ornament of this group suggests that it is probably derived from the Spiriferinae by neotenous retention of an ovate growth form throughout ontogeny. *Mirifusella* Carter is placed here with considerable doubt. Its simple ribbing and sharply delimited fold are not usual for this subfamily.

Stratigraphic Range.—Lower Carboniferous (Tournaisian)–Lower Permian.

Genera Included.—*Purdonella* Reed, 1944; *Ala* Nalivkin, 1979; *Domokhotia* Abramov and Grigor'eva, 1983; *Eliva* Frederiks, 1924; ?*Mirifusella* Carter, 1971; *Neomunella* Ozaki, 1931; *Podtsheremia* Kalashnikov, 1966.

Family Choristitidae Waterhouse, 1968
[*nom. transl.* Ivanova, 1972, p. 40,
ex Subfamily Choristitidinae Waterhouse, 1968, p. 9]

Diagnosis.—Cardinal extremities rounded in juveniles, variable in large adults; denticulation usually well developed; numerous simple or bifurcating costae usually present on entire surface; micro-ornament capillate; delthyrial plate absent; distinctive vascular impressions commonly present, especially in younger genera.

Stratigraphic Range.—Lower Carboniferous–Permian.

Subfamily Angiospiriferinae Legrand-Blain, 1985
[Subfamily Angiospiriferinae Legrand-Blain, 1985, p. 574]

Diagnosis.—Dental adminicula short and close-set or absent; vascular impressions ramiform, or weakly to moderately reticulate; micro-ornament finely cancellate or radially granulose, formed by weak capillae and fine, slightly lamellose growth lines.

Discussion.—This subfamily first appears in the Visean of Eurasia and North Africa and was undoubtedly derived from some member of the Sergospiriferinae by the acquisition of short dental adminicula, distinct vascular impressions, and

weakly capillate micro-ornament. The assignment of *Quizhouspirifer* Xian is tentative because the vascular impressions are unknown.

Stratigraphic Range.—Lower Carboniferous (Visean)–Lower Permian.

Genera Included.—*Angiospirifer* Legrand-Blain, 1985; *Anthracothyrina* Legrand-Blain, 1984; *Brachythyrina* Frederiks, 1929 [=*Anelasmina* Semikhatova, 1939]; *Elinoria* Cooper and Muir-Wood, 1951; *Eobrachythyrina* Lazarev and Poletaev, 1982; *Prochoristitella* Legrand-Blain, 1969; ?*Quizhouspirifer* Xian, 1982.

Subfamily Choristitinae Waterhouse, 1968
[Subfamily Choristitidinae Waterhouse, 1968, p. 9]

Diagnosis.—Dental adminicula close-set, subparallel; vascular impressions reticulate.

Discussion.—*Settedabania* Abramov has an unusual muscle platform in the ventral valve and lacks any indication of vascular markings.

Stratigraphic Range.—?Lower Carboniferous; Upper Carboniferous; ?Lower Permian.

Genera Included.—*Choristites* Fischer de Waldheim, 1825 [=*Alphachoristites* Gatinaud, 1949; ?*Betachoristites* Gatinaud, 1949; *Yatsengina* Semikhatova, 1936]; *Choristitella* Ivanov and Ivanova, 1937; *Parachoristites* Barkhatova, 1968; ?*Settedabania* Abramov, 1970; *Trautscholdia* Ustritsky, 1967.

Subfamily Tangshanellinae Carter, **new subfamily**

Diagnosis.—Outline subovate with rounded cardinal extremities; dental and dorsal adminicula absent; vascular impressions poorly developed or unknown.

Discussion.—The coarse simple lateral plicae of *Capillispirifer* Zhang are not characteristic of this subfamily.

Stratigraphic Range.—Upper Carboniferous–Upper Permian.

Genera Included.—*Tangshanella* Chao, 1929; *Alphaneospirifer* Gatinaud, 1949 [=*Semibrachythyrina* Yang, 1962]; ?*Capillispirifer* Zhang, 1983; *Zhejiangospirifer* Liang, 1982.

Family Imbrexiidae Carter, 1992
[Family Imbrexiidae Carter, 1992, p. 327]

Diagnosis.—Outline transversely subquadrate; cardinal extremities extended in juveniles, variable in adults; fold and sulcus well developed, often medially subangular, flaring anteriorly in some genera; ventral interior with dental adminicula and short delthyrial plate; ornament of moderately numerous simple or bifurcating costae on both flanks and fold-sulcus; micro-ornament of weak capillae and regularly imbricate growth lamellae.

Discussion.—Carter (1992:328) speculated that this family was derived from the Prospirinae because of similarities in macro- and micro-ornament between prospirins and the earliest imbrexiid genus *Fernglenia* Carter.

Stratigraphic Range.—Lower Carboniferous (?Middle, Upper Tournaisian).

Genera Included.—*Imbrexia* Nalivkin, 1937; *Fernglenia* Carter, 1992; *Tegulocrea* Carter, 1992.

Family Trigonotretidae Schuchert, 1893
[*nom. transl.* Carter, herein,
ex Subfamily Trigonotretinae Schuchert, 1893, p. 156]

Diagnosis.—Usually strongly transverse in adult growth stage; fold and sulcus

well developed; denticulate hingeline well developed; entire surface ribbed, often plicate; lateral slopes commonly fasciculate.

Stratigraphic Range.—Lower Carboniferous–Upper Permian.

Subfamily Neospiriferinae Waterhouse, 1968
[Subfamily Neospiriferinae Waterhouse, 1968, p. 9]

Diagnosis.—Weakly to strongly fasciculate; costae medium to fine, nearly uniform in size anteriorly; micro-ornament weakly capillate, often lamellose or imbricate; ventral interior with delthyrial plate.

Discussion.—The genus *Blasispirifer* Kulikov is placed here tentatively on the basis of having a few fasciculate plicae. In addition, its growth form and lack of dental adminicula are not usual for this subfamily. The neospiriferins are likely to have been derived from the Imbrexiidae by acquisition of fasciculate plicae on the flanks.

Stratigraphic Range.—Upper Carboniferous–Upper Permian.

Genera Included.—*Neospirifer* Frederiks, 1924; *Betaneospirifer* Gatinaud, 1949; ?*Blasispirifer* Kulikov, 1950; *Cartorhium* Cooper and Grant, 1976; *Costatispirifer* Archbold and Thomas, 1985; *Crassispirifer* Archbold and Thomas, 1985; *Cratispirifer* Archbold and Thomas, 1985; *Fusispirifer* Waterhouse, 1966 [=*Transversaria* Waterhouse and Gupta, 1983]; *Gibbospirifer* Waterhouse, 1971; *Gypospirifer* Cooper and Grant, 1976; *Imperiospira* Archbold and Thomas, 1993; *Kaninospirifer* Kulikov and Stepanov, 1975; *Lepidospirifer* Cooper and Grant, 1969; *Pondospirifer* Waterhouse, 1978; *Septospirifer* Waterhouse, 1971; *Tibetospirifer* Liu and Wang, 1990.

Subfamily Trigonotretinae Schuchert, 1893
[Subfamily Trigonotretinae Schuchert, 1893, p. 156]

Diagnosis.—Transverse; often thick shelled; fold and sulcus moderately developed; lateral slopes weakly to strongly plicate, variable fasciculate; finer ribbing medium to coarse, often forming unequal ribs anteriorly; micro-ornament capillate and variably cancellate; ventral interior with dental adminicula, obscured by thick apical, commonly bulbous, delthyrial callus.

Discussion.—*Brachythyrinella* Waterhouse and Gupta is tentatively assigned here on the basis of its macro-ornament, which is well illustrated in Thomas (1971:pl. 19). Internally, it differs greatly from the other genera placed here, lacking a delthyrial plate or umbonal callus. *Sulciplica* Waterhouse does not have secondary costae or costellae imposed on the plicae and thus differs from the other genera in this subfamily.

Stratigraphic Range.—Lower Carboniferous (Visean)–Upper Permian.

Genera Included.—*Trigonotreta* Koenig, 1825 [=*Grantonia* Brown, 1953]; *Aperispirifer* Waterhouse, 1968; ?*Brachythyrinella* Waterhouse and Gupta, 1978; *Frechella* Legrand-Blain, 1986; ?*Sulciplica* Waterhouse, 1968.

Family Spiriferellidae Waterhouse, 1968
[*nom. transl.* Carter, herein,
ex Subfamily Spiriferellinae Waterhouse, 1968, p. 9]
[=Family Spiriferellidae Termier, Termier, Lapparant, and Martin, 1974, p. 136]

Diagnosis.—Lateral slopes plicate, coarsely costate, or fasciculate; fold usually with median furrow; delthyrium commonly partially or completely occluded by convex stegidial plates; denticulation poorly developed in narrow hinged genera;

micro-ornament pustulose, commonly capillate; ventral interior with strong short dental adminicula; ventral umbonal region often greatly thickened by callus with deeply impressed ventral muscle field.

Discussion.—*Spiriferellaoides* Lee, Gu, and Li is based on a single poorly preserved specimen. Although it is very difficult to evaluate, it may prove to be a junior synonym of *Spiriferella* and for this reason its assignment here is questioned. *Tipispirifer* Grant is truly enigmatic. Its growth form and macro-ornament of fine costae are unusual for this family. It is assigned here on the basis of its pustulose micro-ornament and stegidial cover of the delthyrium.

The other genera in this family form a close-knit group characterized by thick ventral umbones and a pustulose micro-ornament. They were probably derived from the Trigonotretinae by the acquisition of pustulose micro-ornament.

Stratigraphic Range.—Upper Carboniferous (Bashkirian)–Upper Permian (Vedian).

Genera Included.—*Spiriferella* Chernyshev, 1902; *Alispiriferella* Waterhouse and Waddington, 1982; *Arcullina* Waterhouse, 1986; *Elivina* Frederiks, 1924; *Eridmatus* Branson, 1966; *Plicatospiriferella* Waterhouse and Waddington, 1982; *Rhombospirifer* Duan and Li, 1985; ?*Spiriferellaoides* Lee, Gu, and Li, 1980; *Timaniella* Barkhatova, 1968; ?*Tipispirifer* Grant, 1976.

Superfamily Paeckelmanelloidea Ivanova, 1972
[*nom. correct.* Carter, herein
(*pro* Paeckelmanellacea Ivanova, 1981, p. 22) *nom. trans.* Ivanova, 1981, p. 22, *ex* Paeckelmanellidae Ivanova, 1972, p. 40]

Diagnosis.—Moderately to strongly transverse with maximum width at hingeline; ribs usually simple on flanks, but geologically younger forms sometimes with bifurcations; fold and sulcus smooth or with median rib in sulcus, or more rarely, multicostate; ventral interarea usually moderately to very high, often catacline to slightly procline or weakly apsacline; hingeline denticulate; micro-ornament consisting of capillae and anteriorly free growth lamellae; dental adminicula usually present; vascular markings simple, radial; ctenophoridium present.

Discussion.—The origin of this superfamily is not certain, but it clearly began in the Famennian. The earliest paeckelmanelloid, *Strophopleura* Stainbrook, appeared in the early Upper Famennian, slightly before the earliest true spiriferoids *Parallelora* or *Eobrachythyris*. The denticulate hingeline and capillate micro-ornament point to a close relationship with the Spiriferoidea, probably a shared ulbospiriferid ancestor.

Stratigraphic Range.—Upper Devonian–Upper Permian.

Family Strophopleuridae Carter, 1974
[*nom. trans.* Carter, herein, *ex* Strophopleurinae Carter, 1974, p. 677]

Diagnosis.—Ventral septum absent.

Stratigraphic Range.—Upper Devonian–Upper Permian.

Subfamily Strophopleurinae Carter, 1974
[Subfamily Strophopleurinae Carter, 1974, p. 677]

Diagnosis.—Small, with simple lateral ribs; sulcus smooth or with median rib.

Discussion.—*Calvustrigis* Carter is tentatively placed here because it lacks an imbricate ornament, differing from all other genera assigned here. Although *Iwaispirifer* Tachibana is poorly known and a denticulate hingeline has not been

established, its growth form, close-set dental adminicula, and imbricate-capillate micro-ornament strongly suggest placement here.

Stratigraphic Range.—Upper Devonian (Famennian)–Upper Carboniferous (Moscovian).

Genera Included.—*Strophopleura* Stainbrook, 1947; *Acuminothyris* Roberts, 1963; *Avisyrinx* Martinez Chacon, 1975; ?*Calvustrigis* Carter, 1987; *Cantabriella* Martinez Chacon and Rio Garcia, 1987; ?*Iwaispirifer* Tachibana, 1963; *Voiseyella* Roberts, 1964 [=*Amesopleura* Carter, 1967].

Subfamily Bashkiriinae Nalivkin, 1979
[*nom. trans.* Carter, herein, *ex* Bashkiriidae Nalivkin, 1979, p. 143]

Diagnosis.—Small to medium size; lateral ribs simple; fold and sulcus ribbed; ventral interarea moderately high to very high, often flattened, catacline to procline.

Discussion.—Denticulation in the genus *Adminiculoria* Waterhouse and Gupta has not been established; otherwise, it could be assigned here confidently.

Stratigraphic Range.—Lower Carboniferous.

Genera Included.—*Bashkiria* Nalivkin, 1979; ?*Adminiculoria* Waterhouse and Gupta, 1978; *Celsifornix* Carter, 1974; *Fusella* McCoy, 1844.

Subfamily Pterospiriferinae Waterhouse, 1975
[Subfamily Pterospiriferinae Waterhouse, 1975, p. 15]

Diagnosis.—Medium sized to large; ribs on flanks simple or bifurcating, rarely fasciculate; fold and sulcus smooth or with median rib, rarely costate; dental adminicula short and divergent.

Stratigraphic Range.—Upper Carboniferous–Upper Permian.

Genera Included.—*Pterospirifer* Dunbar, 1955; *Alispirifer* Campbell, 1961; *Haplospirifer* Lee and Gu, 1976; *Pteroplecta* Waterhouse, 1978; *Spiriferinaella* Frederiks, 1926; *Xizispirifer* Liang, 1990.

Family Paeckelmanellidae Ivanova, 1972
[Family Paeckelmanellidae Ivanova, 1972, p. 40]

Diagnosis.—With ventral medium septum; lateral ribs simple.

Stratigraphic Range.—Lower Permian–Upper Permian.

Subfamily Paeckelmanellinae Ivanova, 1972
[*nom. trans.* Waterhouse, 1975, p. 15,
ex Paeckelmanellidae Ivanova, 1972, p. 40]

Diagnosis.—With short divergent dental adminicula.

Stratigraphic Range.—Lower Permian–Upper Permian.

Genera Included.—*Paeckelmanella* Likharev, 1934; *Darvasia* Likharev, 1934; *Odontospirifer* Dunbar, 1955.

Subfamily Scenesiinae Carter, **new subfamily**

Diagnosis.—With short apical delthyrial plate; dental adminicula absent.

Stratigraphic Range.—Lower Permian.

Genus Included.—*Scenesia* Cooper and Grant, 1976.

Superfamily Brachythyridoidea Frederiks, 1924
[*nom. transl.* Carter, herein
(*ex* Brachythyrinae Frederiks, 1924, p. 316)]

Diagnosis.—Outline ovate; hingeline narrow; cardinal extremities rounded in all growth stages; lateral slopes with coarse, usually simple ribbing; fold-sulcus weakly to moderately developed; denticulation not present in younger genera; micro-ornament absent or weakly developed; dental adminicula, subdelthyrial plate, and dorsal adminicula absent; delthyrium partially covered by thin deltidium or stegidial plates.

Discussion.—The suppressed denticulation and lack of capillate micro-ornament suggest that this group may have been derived independently from the theodossioids or an intermediate ancestor by neoteny, with concommitant loss of dental adminicula.

The origin of this superfamily is obscured by the paedomorphically simple internal morphology of the genera included here. Also, the characteristic rounded outline and general absence of micro-ornament of these genera could be construed as either primitive or derived. Assuming that at least some of these characters give an indication of ancestry, it seems possible that this group was derived from a subovate, well-inflated form with a few coarse simple ribs on each lateral slope. Because there is weak denticulation of the hingeline and obscurely capillate micro-ornament in at least one of the geologically early genera, it seems most likely that this group was derived from an offshoot of the same stock that produced the other Late Paleozoic superfamilies of this order, namely, the Theodossioidea.

Stratigraphic Range.—Upper Devonian (Famennian)–Permian.

Family Brachythyrididae Frederiks, 1924
[*nom. transl. et correct.* Pitrat, 1965, p. H706,
ex Subfamily Brachithyrinae Frederiks, 1924, p. 316]

Diagnosis.—Primary median costa in sulcus absent.

Discussion.—*Dalaia* Plodowski was originally assigned by Plodowski (1968: 256) to the Reticulariidae, but it lacks spinose or pitted ornament and cannot be assigned to either the Reticularioidea or Martinioidea. The micro-ornament of *Pustulosplica* Waterhouse consists of discontinuous capillae and elongated fine nodes or pustules, which is unknown in other members of this superfamily. This micro-ornament is reminiscent of several martiniid genera and assignment of *Pustuloplica* here is uncertain.

Stratigraphic Range.—Upper Devonian (Famennian)–Permian (?Kazanian).

Genera Included.—*Brachythyris* McCoy, 1844 [=*Ovalia* Nalivkin, 1937]; *Cathayspirina* Liang, 1990; ?*Dalaia* Plodowski, 1968; *Ella* Frederiks, 1918; *Meristorygma* Carter, 1974; ?*Pustuloplica* Waterhouse, 1968.

Family Skelidorygmidae Carter, **new family**

Diagnosis.—Sulcus with primary median costa, often with additional sulcal costae that bifurcate from sulcus-bounding ribs.

Stratigraphic Range.—Upper Devonian (Famennian)–Upper Carboniferous (Bashkirian).

Genera Included.—*Skelidorygma* Carter, 1974; *Litothyris* Roberts, 1971.

Suborder Delthyridina Ivanova, 1972
[Suborder Delthyridina Ivanova, 1972, p. 41]

Diagnosis.—Lateral slopes plicate, rarely costate; concentric lamellae, if present, fimbriate, spinulose, or exopunctate; early forms with internal plates and septa, tending to become pedomorphically simple in some geologically younger forms; commonly with ctenophoridium.

Stratigraphic Range.—Lower Silurian–Upper Permian.

Superfamily Delthyridoidea Phillips, 1841
[*nom. transl.* Ivanova, 1959, p. 56, *nom. correct.* Johnson, 1970, p. 184
(*ex* Delthyridae Phillips, 1841, p. 54)]

Diagnosis.—Biconvex, with fold and sulcus.
Stratigraphic Range.—Lower Silurian (Upper Llandoverian)–Middle Devonian (Eifelian).

Family Delthyrididae Phillips, 1841
[*nom. correct.* Johnson, 1970, p. 184
(*pro* Delthyridae Phillips, 1841, p. 54)]

Diagnosis.—Small to medium size, pauciplicate; commonly with crural plates.
Stratigraphic Range.—Lower Silurian (Upper Llandoverian)–Middle Devonian (Eifelian).

Subfamily Delthyridinae Phillips, 1841
[*nom. transl., nom. correct.* Johnson, 1970, p. 184
(*ex* Delthyridae Phillips, 1841, p. 54)]

Diagnosis.—Ventral median septum present.
Stratigraphic Range.—Upper Silurian (Wenlockian)–Middle Devonian (Eifelian).
Genera Included.—*Delthyris* (*Delthyris*) Dalman, 1828; *Delthyris* (*Quadrifarius*) Fuchs, 1929; *Ivanothyris* Havlíček, 1957.

Subfamily Howellellinae Johnson and Hou, **new subfamily**

Diagnosis.—Ventral median septum lacking.
Stratigraphic Range.—Lower Silurian (Upper Llandoverian)–Middle Devonian (Eifelian).
Genera Included.—*Howellella* (*Howellella*) Kozlowski, 1946; *Howellella* (*Hysterohowellella*) Carls, 1985; *Howellella* (*Iberohowellella*) Carls, Meyn, and Vespermann, 1993; *Acanthospirifer* Menakova, 1964; *Aldanispirifer* Alekseeva, 1967 [=*Holcospirifer* Bassett, Cocks, and Holland, 1976]; *Howelloidea* Su, 1980; *Orientospirifer* Hou and Xian, 1975; *Pseudokymatothyris* Chen, 1979; *Qiansispirifer* Yang, 1977; *Rufispirifer* Havlíček, 1987; *Xenospirifer* Hou and Xian, 1975.

Family Hysterolitidae Termier and Termier, 1949
[*nom. transl.* Johnson and Hou herein
(*ex* Hysterolitinae Termier and Termier, 1949, p. 95)]

Diagnosis.—Medium to large size; fold and sulcus smooth or plicate; flanks commonly multiplicate; crural plates present or absent.
Stratigraphic Range.—Lower Devonian (Upper Lochkovian)–Middle Devonian (Lower Givetian).

Subfamily Hysterolitinae Termier and Termier, 1949
[Hysterolitinae Termier and Termier, 1949, p. 95]
[=Paraspiriferinae Pitrat, 1965, p. H684]

Diagnosis.—Fold and sulcus smooth; mostly lacking crural plates.
Stratigraphic Range.—Lower Devonian (Upper Lochkovian)–Middle Devonian (Eifelian).

Genera Included.—*Hysterolites* Schlotheim, 1820; *Antispirifer* Williams and Breger, 1916; *Arduspirifer,* Mittmeyer, 1972; *Australospirifer* Caster, 1939; *Brachyspirifer* (*Brachyspirifer*) Wedekind in Salomon, 1926; *Brachyspirifer* (*Torosospirifer*) Gourvennec, 1989; *Costellispirifer* Boucot, 1973 [=*Concinnispirifer* Boucot, 1975]; *Dixonella* Gourvennec, 1989; *Dyticospirifer* Johnson, 1966; *Euryspirifer* Wedekind in Salomon, 1926 [=*Rhenospirifer* Mittmeyer, 1972]; *Otospirifer* Hou and Xian, 1975; *Paraspirifer* Wedekind, 1926; *Patriaspirifer* Johnson, 1995; *Rostrospirifer* Grabau, 1931 [=*Neodelthyris* Hou, 1963]; *Trigonospirifer* Wang, Rong, and Chen, 1987; *Xinjiangospirifer* Hou and Zhang, 1983.

Subfamily Fimbrispiriferinae Pitrat, 1965
[*nom. transl.* Wang, 1979, p. 77
(*ex* Fimbrispiriferidae Pitrat, 1965, p. H687)]

Diagnosis.—Fold, sulcus, and flanks plicate; crural plates present or absent.

Discussion.—Boucot (1975) proposed *Vandercammenina* and *Struveina* as Old World-Realm genera of the Acrospiriferinae, but they are here excluded from that subfamily because of their fimbriate ornament. We regard *Fimbrispirifer,* a Middle Devonian genus from eastern North America, as a descendant of *Struveina* by late migration of that stock, following a pattern demonstrated for the genus *Paraspirifer* (Johnson, 1979).

Stratigraphic Range.—Lower Devonian (Pragian)–Middle Devonian (Lower Givetian).

Genera Included.—*Fimbrispirifer* Cooper, 1942; *Struveina* Boucot, 1975; *Vandercammenina* Boucot, 1975.

Family Acrospiriferidae Termier and Termier, 1949
[*nom. transl.* Johnson and Hou herein
(*ex* Acrospiriferinae Termier and Termier, 1949, p. 96)]

Diagnosis.—Medium to large size, transverse, capillate with fila; crural plates present or absent.

Discussion.—A peculiarity of genera in this family is the presence of fine or prominent capillae together with a concentric ornament of fila. Examples are *Acrospirifer primaevus* as illustrated by Vandercammen (1963:pl. 1, fig. 19, pl. 2, fig. 11), *Acrospirifer fallax* as illustrated by Jahnke (1971:pl. 6, fig. 10), and *Mauispirifer hectori* as illustrated by Allan (1947:pl. 62, fig. 6). Capillae are so well developed on *Multispirifer* that it was originally presumed to be an eospiriferid (Kaplun, 1961:88). The capillae of *Costispirifer* caused Ivanova (1972) to suppose that it was derived from the eospiriferids. Of particular interest is the ornament of *Euryspirifer* Wedekind, 1926. Vandercammen (1963:pl. 8, fig. 6) and Jahnke (1971:pl. 7, fig. 4c) both show an ornament of capillae interrupted by fila. This type of ornament is especially well represented by *Euryspirifer atlanticus,* as illustrated by Boucot (1973:pl. 17, fig. 9).

Stratigraphic Range.—Lower Devonian (Upper Lochkovian)–Middle Devonian (Eifelian).

Subfamily Acrospiriferinae Termier and Termier, 1949
[Acrospiriferinae Termier and Termier, 1949, p. 96]

Diagnosis.—Flanks strongly plicate, delthyrium lacking apical deltidium; dental plates strong or partly buried in umbonal callus; ctenophoridium on floor of notothyrial chamber attached to myophragm, or elevated.

Stratigraphic Range.—Lower Devonian (Upper Lochkovian–Emsian).
Genera Included.—*Acrospirifer* Helmbrecht and Wedekind, 1923; *Mauispirifer* Allan, 1947; *Xerospirifer* Havlíček, 1978.

Subfamily Costispiriferinae Termier and Termier, 1949
[Costispiriferinae Termier and Termier, 1949, p. 98]

Diagnosis.—Multiplicate, with narrow interspaces; ventral interarea low, trapezoidal; broad delthyrium with apical deltidium; fold and sulcus smooth or plicate; flanks with simple plications; short, widely spaced dental plates, partly buried in umbonal callus; sockets strong, simple, curved; ctenophoridium not built up.
Discussion.—Although *Cumberlandina* was originally assigned to the Mucrospiriferinae by Boucot (1975:371), that assignment cannot be sustained because *Cumberlandina* lacks lamellose concentric ornament. Except for the lack of plications on the fold and sulcus, *Cumberlandina* closely resembles *Costispirifer.*
Stratigraphic Range.—Lower Devonian (Pragian).
Genera Included.—*Costispirifer* Cooper, 1942; *Cumberlandina* Boucot, 1975.

Family Elymospiriferinae Johnson and Hou, **new subfamily**

Diagnosis.—Fold and sulcus plicate; flanks with bifurcating plications.
Stratigraphic Range.—Lower Devonian (Pragian)–Middle Devonian (Eifelian).
Genera Included.—*Elymospirifer* Wang, 1974; *Borealispirifer* Hou and Su, 1993; *Multispirifer* Kaplun, 1961; *Perryspirifer* Jones and Boucot, 1983.

Family Cyrtinopsidae Wedekind, 1926
[*nom. transl.* Boucot, 1957, p. 38
(*ex* Cyrtinopsinae Wedekind in Salomon, 1926, p. 198)]

Diagnosis.—Frilly growth lamellae, with interrupted capillae; ctenophoridium lacking or, in younger genera, rudimentary.
Stratigraphic Range.—Upper Silurian (Wenlockian)–Middle Devonian (Givetian).

Subfamily Cyrtinopsinae Wedekind, 1926
[Cyrtinopsinae Wedekind in Salomon, 1926, p. 198]
[=Kozlowskiellininae Boucot, 1958, p. 1031
(*nom. correct.* Kozlowskiellinae Boucot, 1957, p. 317)]

Diagnosis.—With ventral median septum.
Stratigraphic Range.—Upper Silurian (Wenlockian)–Middle Devonian (Givetian).
Genera Included.—*Cyrtinopsis* Scupin, 1896; *Kozlowskiellina* Boucot, 1958; *Megakozlowskiella* Boucot, 1957; *Plicocyrtina* Havlíček, 1956.

Subfamily Araspiriferinae Johnson, **new subfamily**

Diagnosis.—Without ventral median septum.
Stratigraphic Range.—Upper Silurian (Wenlockian–Ludlovian).
Genera Included.—*Araspirifer* Havlíček, 1987; *Boucotinskia* Brunton and Cocks, 1967.

Family Mucrospiriferidae Boucot, 1959
[*nom. transl.* Johnson and Carter herein
(*ex* Mucrospiriferinae Boucot, 1959. p. 745)]

Diagnosis.—Lamellose growth lines; ctenophoridium without crural plates.

Stratigraphic Range.—Middle Devonian (Givetian)–Lower Carboniferous (Visean).

Subfamily Mucrospiriferinae Boucot, 1959
[Mucrospiriferinae Boucot, 1959, p. 745]

Diagnosis.—Transverse, multiplicate; dental plates present or absent; without median septum.

Stratigraphic Range.—Middle Devonian (Givetian)–Upper Devonian (Famennian).

Genera Included.—*Mucrospirifer* Grabau, 1931 [=*Lamellispirifer* Nalivkin, 1937; *Khinganospirifer* Su, 1976]; *Apousiella* Carter, 1972 [=*Bouchardopsis* Mailleux, 1933]; *Eleutherokomma* Crickmay, 1950 [=*Dmitrispirifer* Liashenko, 1973; *Sculptospirifer* Su, 1980]; *Sulcatospirifer* Maxwell, 1954.

Subfamily Tylothyridinae Carter, 1972
[Tylothyridinae Carter, 1972, p. 730]

Diagnosis.—Variable outline and moderately numerous lateral costae; radial ornament apparently lacking; with dental plates and median septum.

Stratigraphic Range.—Middle Devonian (Upper Givetian)–Lower Carboniferous (Visean).

Genera Included.—*Tylothyris* North, 1920 [=*Welleria* Mailleux, 1931]; *Texathyris* Carter, 1972.

Superfamily Reticularioidea Waagen, 1883
[*nom. correct.* Gourvennec and Carter, herein
(*pro* Reticulariacea Waagen, 1883, *nom. transl.* Pitrat, 1965, p. H717,
ex Subfamily Reticulariinae Waagen, 1883, p. 538)]

Diagnosis.—Subequally biconvex; outline generally transversely subovate to equidimensional; hinge line short, lateral extremities rounded; fold and sulcus generally present, commonly weakly developed; ribbing absent or weak, rarely multicostate; micro-ornament often lamellose, commonly with fine spines or granules.

Stratigraphic Range.—Silurian (Upper Llandovery)–Upper Permian.

Family Reticulariidae Waagen, 1883
[*nom. transl.* Ivanova, 1959, p. 56,
ex Subfamily Reticulariinae Waagen, 1883, p. 538]

Diagnosis.—Lateral slopes commonly smooth, rarely plicate; fold and sulcus, if present, smooth; micro-ornament concentrically arranged, consisting of growth lamellae and generally uniramous spinules or fine tubercles; dental adminicula generally present, true ventral septum absent, median ridge or myophragm present in some genera.

Discussion.—This diagnosis is based on the assumption that *Reticularia* lacks a true ventral septum but, rather, possesses a median ridge or euseptoid, as described and illustrated by George (1932:552). If this is actually not the case, then the following classification is incorrect and we would be compelled to reassign all of the nonseptate genera to a different family and revise the composition of the Xenomartiniidae.

Stratigraphic Range.—Silurian (Upper Llandovery)–Upper Permian.

Subfamily Reticulariinae Waagen, 1883
[Subfamily Reticulariinae Waagen, 1883, p. 538]

Diagnosis.—Generally pauciplicate; lacking delthyrial plates, delthyrial ridges or any kind of apical thickening; commonly lacking crural plates.

Discussion.—Havlíček erected the genus *Undispirifer* in 1957 and designated *S. undiferus* Roemer 1844 as type species. He pointed out the presence of a well-developed fold and sulcus and low lateral plications, which are commonly only perceptible anteriorly. In 1959, he added "basal plates do not meet the floor of the valve" and "without subdelthyrial plate" (in the comparison with *Eoreticularia*). In 1967, Vandercammen gave illustrations of the original material of Roemer, considering *undiferus* and *gerolsteinites* Steininger, 1853, as synonyms (form I and II of the species *undiferus,* p. 6). His figure shows a specimen labeled "Original *Sp. undiferus* F. Roemer" but Vandercammen indicated that this specimen probably is not the type, which was apparently lost (there are effectively some differences with the original illustration by Roemer). The origin of the label is unknown. This specimen seems closely related to the type of *S. curvata undulata* Roemer, 1844 (pl. 4, fig. 5a, b) which was later designated as the type of *S. gerolsteinensis* by Steininger (1853). Recently, Struve (1990) erected the genus *Gerolsteinites,* with *Spirifera gerolsteinensis* Steininger as the type species, and which is distinguished from *Undispirifer* by: 1) a well-marked fold and sulcus, 2) plicae expressed from apex to commissure, and 3) a high ventral interarea. These arguments do not justify the erection of a new genus because the original diagnosis of *Undispirifer* states that there is a well-developed sulcus/fold and lateral plications are often (but not necessarily) only perceptible anteriorly. In addition, the original illustration by Roemer (1844:pl. 4, fig. 6a–c) shows *undiferus* with a well-developed, if not high, ventral interarea, not far in its form from that of *S. gerolsteinensis* (=*S. curvatus undulata*). It is clear that the characters of the genus *Undispirifer* show some variability, but the erection of a new genus does not appear as a necessity (*Gerolsteinites* at most should have subgeneric rank). In any case the problem of the type is not solved. Some other features illustrate the variability in this genus. According to Havlíček (1959:254), *Undispirifer* is devoid of a delthyrial plate. However, some authors have mentioned such a plate, following Vandercammen (1957:6), who indicated that a delthyrial plate is present but difficult to identify. There is a possibility that the specimen described by Vandercammen belongs to another genus, e.g., *Rhenothyris,* because his description of the species states that some large mature specimens are smooth (1957:5). Otherwise, although *Undispirifer* generally lacks crural plates and possesses only plate-like crural bases (Havlíček, 1959:254), it seems that in some specimens these plates join the floor of the valve (Johnson, 1974:pl. 10, fig. 4). The preceding discussion shows that a revision of the species *undiferus* and the designation of a neotype are desirable. Because there is still doubt about the presence or absence of a delthyrial plate, the genus is assigned here with a question mark.

The subgenus *Nakazatothyris* Minato and Kato, 1977 is also placed in synonymy of the genus *Undispirifer* for reasons comparable to the ones mentioned above: its characters (few plicae better expressed in the vicinity of the fold/sulcus and near the apex) do not justify the erection of a (sub-)genus because they fall within a reasonable variation of the genus *Undispirifer. Undispiriferoides* Xian is poorly known and its status is not clear.

Stratigraphic Range.—Lower Devonian (Upper Pragian)–Upper Permian.

Genera Included.—*Reticularia* McCoy, 1844; ?*Georgethyris* Minato, 1953;

Parareticularia Lee and Gu, 1976; *Squamularia* Gemmellaro, 1899; ?*Undispirifer* Havlíček, 1957 [=Nakazatothyris Minato and Kato, 1977] [=Gerolsteinites Struve, 1990]; ?*Undispiriferoides* Xian, 1978.

Subfamily Reticulariopsinae Gourvennec, **new subfamily**

Diagnosis.—Generally pauciplicate; lacking delthyrial plates, dethyrial ridges or any kind of apical thickening; dental plates, crural plates and ctenophoridium present.

Discussion.—The serial sections accompanying the original diagnosis of *Paraquadrithyris* are aberrant and probably erroneous. No comments are given by the author about the cardinal process, but the genus is compared with *Tingella* (=*Reticulariopsis*), which possesses a ctenophoridium. After Hou, the two genera are probably synonyms.

Vandercammen (1958) does not recognize the genus *Reticulariopsis,* which he considers as insufficiently described, but he accepts *Tingella* Grabau, in which he places *R. dereimsi,* the type species of *Reticulariopsis.* Vandercammen assigned two other species to *Tingellas* (*reticularioides* and *concentrica*). The material described under the name of *concentrica* by Vandercammen has since been recognized as *Gerothyris eifliana,* while *T. dereimsi* (*sensu* Vandercammen) has been found only in Belgium and differs from the Spanish species described by Oehlert and Oehlert (1901), which lacks a delthyrial plate. Furthermore, the type species of *Tingella, T. reticularioides,* apparently also lacks a delthyrial plate. Thus *Tingella* is a junior synonym of *Reticulariopsis* and the interpretation of Vandercammen (delthyrial plate present) is to be rejected (this latter material probably belongs to *Rhenothyris*).

Stratigraphic Range.—Silurian (Wenlock)–Middle Devonian (Givetian).

Genera Included.—*Corylispirifer* Gourvennec, 1989; *Kymatothyris* Struve, 1970 [=Fallaxispirifer, Su 1976]; *Mariaspirifer* Cherkesova, 1991; ?*Paraquadrithyris* Yang, 1983; *Padvenia* Breivel and Breivel, 1988; *Proreticularia* Su, 1990; *Prosserella* Grabau, 1910; *Reticulariopsis* Frederiks, 1916 [=*Tingella* Grabau, 1931]; *Yeothyris* Struve, 1992.

Subfamily Rhenothyridinae Gourvennec, **new subfamily**

Diagnosis.—With delthyrial plate, ridge or ventral apical thickening; dental plates and ctenophoridium present.

Discussion.—*Rhenothyris* does not possess a true delthyrial plate but only clearly expressed subdelthyrial plates or ridges on internal molds. The definition of the genus *Eohowellella* is imprecise and not in accordance with the insufficient illustrations. For example, the "ventral septum" recorded in the diagnosis is absent on the serial sections; if such a septum is really present, *Eohowellella* would better be assigned to the Quadrithyridinae. The comparison with *Howellella* suggests that a ctenophoridium is present although it is not reported in the diagnosis. The mention of a "finely punctate shell" in the description is probably erroneous(?); such a character would remove *Eohowellella* from the Reticularioidea. For all these reasons, *Eohowellella* is assigned here with doubt.

The ctenophoridium is not reported in the diagnosis of *Nordella* and does not appear in serial sections, but the comparison with *Elita* suggests close analogies in the internal structures, and we admit to the presence of a ctenophoridium. Should this not be the case, *Nordella* would be better placed in the Eoreticulariinae.

Puanospirifer is poorly known; many characters have been "estimated" or ex-

trapolated from the author's comparison with *Reticulariopsis* (particularly for internal structures).

The holotype, paratypes, and figured specimens of *Spirinella* were destroyed by fire in 1953. Strusz (1984) has given a new diagnosis and good illustrations of topotype material, but failed to designate a neotype. We propose to designate the specimen "SUP 55596" (Yass Formation, New South Wales), figured in Strusz (1984:fig. 18A–D) as the lectotype for *Spirinella caecistriata* Johnston (type species of the genus *Spirinella*). Apparently, following the serial sections given by Johnston (1941, fig. 2), *Spirinella* possesses incipient delthyrial plates or ridges. Nevertheless, these structures are poorly expressed and they are not reported by Strusz (1984), who revised the species. Consequently, this genus is assigned here with some doubt. If delthyrial plates and an apical thickening are lacking in *Spirinella,* the Reticulariopsinae would be a better receptacle for this genus.

Stratigraphic Range.—Silurian (?Upper Llandovery, Lower Ludlow)–Middle Devonian (Eifelian, ?Lower Frasnian).

Genera Included.—*Rhenothyris* Struve, 1970; *Deltospirifer* Wang and Rong, 1986; ?*Eohowellella* Lopushinskaja, 1976; *Gerothyris* Struve, 1970; *Grebenella* Modzalevskaia and Besnosova, 1992; ?*Nordella* Liashenko, 1973; *Pseudoundispirifer* Zhang, 1987; ?*Puanospirifer* Jiang, 1978; ?*Spirinella* Johnston, 1941 [=*Ectatoglossa* Chu, 1974]; *Warrenella (Warrenella)* Crickmay, 1953 [=*Minatothyris* Vandercammen, 1957]; *Warrenella (Warrenellina)* Brice, 1982.

Subfamily Obesariinae Gourvennec, **new subfamily**

Diagnosis.—Smooth; lacking dental plates and ctenophoridium; apical thickening in the ventral valve.

Discussion.—*Quasimartinia* occasionally possesses a sinus on the dorsal valve, which is quite uncommon in the Reticularioidea.

In the original diagnosis of *Uexothyris,* no mention is made of a ctenophoridium, so we consider it to be lacking. Nevertheless, Struve (1992:574) placed this genus in the Tribe Gerothyridini with *Gerothyris* and "*Minatothyris,*" both of which possess a ctenophoridium. In the description of the species assigned to *Uexothyris,* the cardinal process is not taken into consideration and no illustration is given. If *Uexothyris* should prove to possess a ctenophoridium, it should be rejected from the Obesariinae and attached to the Rhenothyridinae, hence the question mark in our assignment.

Echinocoeliopsis is assigned here because of its ornament and lack of dental plates, but it is apparently devoid of an apical thickening. Another peculiar feature of this genus is the presence of a bifid shaft supporting the cardinal process. In some respects (size, form, mode of folding, bifid cardinal process) this genus evokes the Ambocoeliidae, particularly *Metaplasia* and allied genera. Otherwise, *Echinocoeliopsis* is only known by a few very small specimens.

Stratigraphic Range.—Silurian (Upper Wenlock)–Middle Devonian (Eifelian).

Genera Included.—*Obesaria* Havlíček, 1957; *Alaskospira* Kirk and Amsden, 1952 [=*Proreticularia* Havlíček, 1957]; *Quasimartinia* Havlíček, 1959 [=*Candispirifer* Havlíček, 1971]; ?*Uexothyris* Struve, 1992; ?*Echinocoeliopsis* Hamada, 1968.

Subfamily Eoreticulariinae Gourvennec, **new subfamily**

Diagnosis.—Smooth; with cardinal platform or septalium; ctenophoridium absent.

Discussion.—A mistake occurs in the translation to English of the work of

Nalivkin (1930:198) concerning *Eoreticularia*: "spines sometimes absent" should read "spines always absent" as is evident from the rest of the description. *Eoreticularia* is distinguished from both *Reticulariopsis* and *Reticularia* by the lack of spines. Havlícek (1971) notes the presence of radially aligned granules and the absence of marginal spines. The sections given by this author (1959:160, 163–164) show a septalium and delthyrial plate, but a ctenophoridium is absent.

Stratigraphic Range.—Silurian (Wenlock)–Upper Devonian (Frasnian).

Genera Included.—*Eoreticularia* Nalivkin in Frederiks, 1924; *Chnaurocoelia* Johnson, Boucot, and Murphy, 1976; *Vadum* Strusz, 1982.

Family Xenomartiniidae Havlíček, 1971
[Xenomartiniidae Havlíček, 1971, p. 24]

Diagnosis.—With ventral median septum.

Discussion.—In his conception of the family, Havlíček emphasized the lack of dental plates (1971:23). Here we would rather emphasize the presence of a ventral septum, which leads us to include the subfamilies Bojothyridinae and Quadrithyridinae and reject the *Obesaria* group. Close affinities exist between the Obesariinae and Xenomartiniidae, so that the latter probably were derived from the Obesariinae by acquisition of a ventral median septum.

Stratigraphic Range.—Upper Silurian–Middle Devonian.

Subfamily Xenomartiniinae Havlíček, 1971
[*nom. transl.* Gourvennec herein (*ex* Xeonmartiniidae Havlíček, 1971, p. 24)]

Diagnosis.—Smooth; lacking dental plates and ctenophoridium.

Discussion.—In 1953, Havlíček described the genus *Xenomartinia* (type species *X. monosepta*) including smooth forms with reticulate ornament and a ventral septum but lacking dental plates. In the same year Minato proposed the genus *Sinothyris* (type species *R. maureri*) with the following definition: "without dental plates but with median septum in the ventral valve." This diagnosis corresponds to that of *Xenomartinia,* and thus the two genera would appear to be synonyms. On the other hand, Minato's interpretation of the species *maureri* is clearly erroneous (Pitrat, 1965:H717), and this leads to some confusion in the definition of the genus *Sinothyris.* Pitrat placed *Sinothyris* in the synonymy of *Reticularia* with some doubt, but we now know that *Reticularia* possesses a myophragm or euseptoid rather than a true septum. The real question is one of priority. After inquiry, we have established that the work by Minato was published on September 30, 1953, while that of Havlíček was published in February 1953. Thus, *Sinothyris* is a junior synonym.

Stratigraphic Range.—Lower (Pragian)–Middle (Eifelian) Devonian.

Genera Included.—*Xenomartinia* Havlíček, 1953 [=*Sinothyris* Minato, 1953].

Subfamily Bojothyridinae Havlíček, 1990
[*nom. transl.* Gourvennec herein
(*ex* Bojothyrididae Havlíček, 1990, p. 186)]

Diagnosis.—With dental plates converging to median septum, commonly producing spondylium or spondylium-like structure.

Discussion.—Although it was first described as lacking dental plates (Havlíček, 1959:244), serial sections in *Quadrithyrina* apparently show tracks of rudimentary dental plates (or ridges) converging towards a septum. Thus, it is assigned here to the Bojothyridinae. On the other hand, the reduced size of these plates and the

apparently smooth cardinal process suggest strong affinities with the Xenomartiniinae. The same applies for *Uralospirifer* in which the dental plates are also reduced but seem somewhat more prominent than in *Quadrithyrina*. The two genera have an almost identical internal structure as pointed out by Havlíček (1959:142). *Uralospirifer* and *Altajella* are also very close externally, but the latter possesses a spondylium and crurual plates and lacks an apical thickening of the shell. The genus *Altajella* can be seen as a possible ancestor of both the Bojothyridinae and Xenomartiniinae.

Stratigraphic Range.—Upper Silurian (Upper Ludlow)–Middle (Eifelian) Devonian.

Genera Included.—*Bojothyris* Havlíček, 1959; *Altajella* Kulkov, 1962; ?*Quadrithyrina* Havlíček, 1959; *Spondylothyris* Su, 1980.

Subfamily Quadrithyridinae Gourvennec, **new subfamily**

Diagnosis.—With divergent or subparallel dental plates.

Discussion.—The commissure of *Quadrithyris* is sometimes strongly uniplicate. The crural plates are apparently lacking, but in some species (e.g., *Q. robusta, Q. orba*) small incipient crural plates are discernible on the bottom of the valve in serial sections. The redefinition of the genus by Boucot (1962) differs somewhat from the original definition. Some elements of this redefinition (e.g., the presence of crural plates) have been accepted in our diagnosis.

Stratigraphic Range.—Upper Silurian (Upper Wenlock)–Middle Devonian (Givetian).

Genus Included.—*Quadrithyris* Havlíček, 1957.

Family Thomasariidae Cooper and Dutro, 1982
[Thomasariidae Cooper and Dutro, 1982, p. 102]

Diagnosis.—Small, hemipyramidal shells, with strong, long dental plates and a pair of conjunct apical plates. Dorsal interior with ctenophoridium, lacking crural plates. Surface with growth lines and fine spines.

Stratigraphic Range.—Upper Devonian (Frasnian).

Genus Included.—*Thomasaria* Stainbrook, 1945.

Family Elythidae Frederiks, 1924
[*nom. transl.* Pitrat, 1965, p. H721,
ex Subfamily Elythinae Frederiks, 1924, p. 304]

Diagnosis.—Lateral slopes smooth or with low plications; fold and sulcus, if present, usually weakly developed; micro-ornament of fine biramous spines.

Discussion.—The development of biramous spines in this family is unique or synapomorphous and appears early in the history of the superfamily.

Stratigraphic Range.—Middle Devonian–Upper Permian.

Subfamily Elythinae Frederiks, 1924
[Subfamily Elythinae Frederiks, 1924, p. 304]

Diagnosis.—Spines biramous but not elaborate; ventral interior with dental adminicula and median ridge; dorsal interior with ctenophoridium.

Stratigraphic Range.—Lower Devonian–Lower Carboniferous.

Genera Included.—*Elita* Frederiks, 1918; *Kitakamithyris* Minato, 1951.

Subfamily Martinothyridinae Carter, **new subfamily**

Diagnosis.—Ventral interior with dental adminicula; ventral median ridge absent; spines elaborate.

Stratigraphic Range.—Lower Carboniferous–Lower Permian.

Genera Included.—*Martinothyris* Minato, 1953; *Latiplecus* Lee and Gu, 1976; *Orenburgella* Pavlova, 1969.

Subfamily Phricodothyridinae Caster, 1939
[*nom. correct.* Carter, herein,
pro Subfamily Phricodothyriinae Caster, 1939, p. 145]

Diagnosis.—Lacking dental adminicula and ventral median ridge; spines elaborate.

Stratigraphic Range.—Lower Carboniferous–Upper Permian.

Genera Included.—*Phricodothyris* George, 1932 [=?*Bajkuria* Ustritsky, 1963; *Condrathyris* Minato, 1953; *Neophricodothyris* Likharev, 1934]; *Astegosia* Cooper and Grant, 1969; *Bullarina* Jing and Sun, 1981; *Nebenothyris* Minato, 1953; *Permophricodothyris* Pavlova, 1965.

Subfamily Toryniferinae Carter, **new subfamily**

Diagnosis.—Dental adminicula and low median ridge present; ctenophoridium absent; spines elaborate.

Stratigraphic Range.—Lower Carboniferous (Tournaisian)–Permian.

Genera Included.—*Torynifer* Hall and Clarke, 1893; *Plicotorynifer* Abramov and Solomina, 1970; *Spirelytha* Frederiks, 1924; *Stepanoviina* Zavadovsky, 1968; *Taimyrella* Ustritsky, 1963; *Toryniferella* Weyer, 1967.

Subfamily Anomaloriinae Cooper and Grant, 1976
[*nom. transl.* Carter, herein
(*ex* Family Anomaloriidae Cooper and Grant, 1976, p. 2260)]

Diagnosis.—Delthyrium covered with convex psuedodeltidium; ventral interior with converging thickened dental flanges that fuse apically; dorsal interior with notothyrial flanges fused to inner socket ridges that partially obscure sockets medially.

Stratigraphic Range.—Permian.

Genera Included.—*Anomaloria* Cooper and Grant, 1969; *Zhinania* Liang, 1990.

Order Spiriferinida Ivanova, 1972
[*nom. trans.* Carter and Johnson, herein
(*ex* Suborder Spiriferinidina Ivanova, 1972, p. 41)]
[=Order Spiriferinida Cooper and Grant, 1976, p. 2666]

Diagnosis.—Hingeline strophic; commonly transverse and biconvex; flanks ribbed, rarely smooth; ventral valve inflated and thicker than dorsal valve; ventral interarea commonly well developed; brachidium, where present, spiraliform, spiralia directed laterally or posterolaterally; jugum generally present; shell punctate.

Discussion.—Punctate spiriferids first appear near the Silurian–Devonian boundary as the distinctive small hemipyramidal genus *Cyrtina* Davidson. The growth form and complex internal structures of this genus indicate that it is morphologically highly specialized and may not reflect the ancestral stock from which this large group is derived. The immediate ancestors of the punctate spiriferids must have been strophic biconvex punctate orthids or impunctate spirifer-

ids with ventral sulcus and dorsal fold. Lacking recognizable antecedents, whether or not these close ancestors were punctate or impunctate cannot be demonstrated.

The Suborder Cyrtinidina comprises three superfamilies, the Cyrtinoidea, Suessioidea, and Spondylospiroidea, all characterized by having spondylia or related adductor-raising platforms. The Suessioidea were derived from the cyrtinoids in the Early Carboniferous, but the Carboniferous and Permian record is poor. The suessioids survived the Permian extinction event and flourished during the Middle and Late Triassic, when they became extinct. Sometime in the Early or very early Middle Triassic a stock of suessioids, the Spondylospiroidea, developed a unique crenulated hingeline. This short-lived group also disappeared in the Late Triassic.

The other punctate suborder, the Spiriferinidina, appeared in the Late Devonian as two distinct lineages, the superfamilies Pennospiriferinoidea and Syringothyridoidea, both derived from the cyrtinids at about the same time. These groups secondarily evolved a spiriferid growth form and discrete dental adminicula in the ventral valve. The syringothyridoids attained large size and survived until the Permian extinction event. The Pennospirinoidea developed a strong ventral median septum and became highly diverse throughout the Permian, but disappeared in the early Triassic, giving rise in the Middle Triassic to the last of the punctate superfamilies, the Spiriferinoidea. The latter group acquired its rounded growth form and reduced radial ornament, reminiscent of the reticularioids, by neoteny.

Stratigraphic Range.—Lower Devonian (Lower Lochkovian)–Lower Jurassic.

Suborder Cyrtinidina Carter and Johnson, **new suborder**

Diagnosis.—Lateral slopes plicate or smooth; ventral valve high, subconical or hemipyramidal in early forms, variable in later ones; delthyrium commonly covered in early genera, variably covered in late genera; ventral interior commonly with elevated adductor attachment structures.

Stratigraphic Range.—Lower Devonian–Lower Jurassic.

Superfamily Cyrtinoidea Frederiks, 1911
[*nom. transl.* Johnson, 1966, p. 177
(*ex* Cyrtininae Frederiks, 1911)]

Diagnosis.—Ventral valve hemipyramidal, with high interarea; dorsal valve flat or weakly convex; nonfimbriate and noncapillate; ventral median septum.

Stratigraphic Range.—Lower Devonian (basal Lochkovian)–Lower Carboniferous (Visean).

Family Cyrtinidae Frederiks, 1911
[*nom. transl.* Stehli, 1954, p. 350
(*ex* Cyrtininae Frederiks, 1911, p. 5)]

Diagnosis.—Stout, apically perforated deltidium; spondylium and divided trichorhinum; bilobed, commonly nonstriate cardinal process, but ctenophoridium may form in older growth stages.

Discussion.—We hypothesize that *Cyrtina,* the oldest genus of the Superfamily Cyrtinoidea, if not derived from an unknown punctate orthid or intermediate, was derived from one of the small impunctate Silurian genera of the Cyrtinopsinae in the Superfamily Delthyridoidea, possibly *Kozlowskiellina* Boucot, 1958. However, demonstrating homology between *Cyrtina* and impunctate taxa is not easy because general morphological similarity can indicate convergent or parallel evolution, as well as a genetic relationship.

Cyrtina became abundant at the beginning of the Devonian, already fully developed with endopunctate shell and tichorhinum. *Kozlowskiellina* is a small, lamellose, cyrtinaform genus with conjunct delthyrial plates pierced by an apical foramen. It has a ventral median septum and dental plates, and a bifid cardinal process in the dorsal valve. We assume that *Kozlowskiellina* could have given rise to *Cyrtinopsis* at about the same time that *Cyrtina* appeared, at the beginning of the Devonian. *Cyrtinopsis* differs from *Kozlowskiellina* by the presence of a spondylium pierced by a median septum and details of micro-ornament and is closer to *Cyrtina* in this way (Havlícek, 1959:144–145; Johnson, 1970:pl. 72, fig. 21–29). *Cyrtina* could have split off from the *Kozlowskiellina–Cyrtinopsis* phylogeny by the acquisition of an endopunctate shell structure and a tichorhinum.

Stratigraphic Range.—Lower Devonian (basal Lochkovian)–Lower Carboniferous (Visean).

Genera Included.—*Cyrtina* Davidson, 1858 [=*Spinocyrtina* Frederiks, 1916; *Cyrtinaellina* Frederiks, 1926; *Trochalocyrtina* Wright, 1975]; *Cyrtinaella* Frederiks, 1916; *Squamulariina* Frederiks, 1916 [=*Pyramidalia* Nalivkin, 1947]; *Tecnocyrtina* Johnson and Norris, 1972.

Family Komiellidae Johnson and Blodgett, 1993
[Family Komiellidae Johnson and Blodgett, 1993, p. 952]

Diagnosis.—Spondylium, or dental flanges and median septum not connected, lacking a tichorhinum; simple, nonstriate cardinal process; jugum sessile.

Discussion.—The name *Komiella* Barkhatova, 1970 (p. 62, footnote) is a *nomen nudum.*

Stratigraphic Range.—Lower Devonian (Emsian)–Upper Devonian (Frasnian).

Genus Included.—*Komiella* Liashenko, 1985.

Superfamily Suessioidea Waagen, 1883
[*nom. correct.* Carter, herein
(*pro* Superfamily Suessiacea Waagen, 1883) *nom. trans.* Pitrat, 1965, p. H675,
ex Subfamily Suessiinae Waagen, 1883, p. 498]

Diagnosis.—Usually cyrtiniform; ventral valve usually hemipyramidal to subconical with high interarea; ventral median septum present, discrete dental adminicula absent; endopunctae or hemipunctae obscure in some genera.

Discussion.—In this superfamily there is an obvious relationship between the hemipyramidal or subconical growth form and internal structures of the ventral valve, namely the adductor-shortening structures such as the spondylium. The poor Paleozoic record of this superfamily hinders interpretation of relationships with the Cyrtinoidea from which the suessioids were derived, probably in the Lower Carboniferous. The Davidsoninidae are unique in this superfamily in being very large, in probably lacking crural processes and a brachidium, and in having hemipunctae. The Davidsoninidae are the only Carboniferous representatives of the Suessioidea, but if one invokes Dollo's Law they were probably not in the direct line of ancestry of the Laballidae, which first appear in the Upper Permian of China with normal brachidial structures intact.

Stratigraphic Range.—Lower Carboniferous (Visean)–Lower Jurassic.

Family Davidsoninidae Ivanova, 1972
[Family Davidsoninidae Ivanova, 1972, p. 41]

Diagnosis.—Lateral slopes ribbed; ventral interior with false spondylium com-

posed of median septum and high dental flanges; ventral adminicula absent; shell substance punctate, but punctae possibly not penetrating primary layer (hemipunctate); jugum and jugal processes absent; brachidium unknown, possibly absent.

Stratigraphic Range.—Lower Carboniferous (Visean–Namurian).

Genera Included.—*Davidsonina* Schuchert and LeVene, 1929; *Carbocyrtina* Ivanova, 1975.

Family Laballidae Dagis, 1962
[*nom. trans.* Dagis, 1965, p. 91,
ex Subfamily Laballinae Dagis, 1962, p. 49]

Diagnosis.—Cyrtiniform; spondylium bisected by high median septum.

Discussion.—This family appears cryptogenically with the genus *Eolaballa* Liao and Meng in the Upper Permian of China.

Stratigraphic Range.—Upper Permian–Upper Triassic.

Subfamily Laballinae Dagis, 1962
[Subfamily Laballinae Dagis, 1962, p. 49]

Diagnosis.—Fold and sulcus well defined; lateral slopes smooth or with one or two faint plicae; delthyrium open.

Stratigraphic Range.—Upper Permian–Upper Triassic.

Genera Included.—*Laballa* Moisseiev, 1962; *Eolaballa* Liao and Meng, 1986; *Pseudolaballa* Dagis, 1974.

Subfamily Spinolepismatininae Carter, **new subfamily**

Diagnosis.—Lateral slopes distinctly plicate; fold and sulcus smooth; micro-ornament densely spinulose.

Stratigraphic Range.—Upper Triassic.

Genera Included.—*Spinolepismatina* Dagis, 1974; *Klipsteinella* Dagis, 1974; *Klipsteinelloidea* Sun, 1981.

Subfamily Paralepismatininae Carter, **new subfamily**

Diagnosis.—Fold and sulcus poorly developed; entirely ribbed; micro-ornament absent.

Stratigraphic Range.—Middle Triassic (Anisian).

Genus Included.—*Paralepismatina* Yang and Xu, 1966.

Family Bittnerulidae Schuchert, 1929
[*nom. trans.* Carter, herein
(*ex* Subfamily Bittnerulinae Schuchert, 1929, p. 21)]
[=Subfamily Thecocyrtellinae Dagis, 1965, p. 105]

Diagnosis.—Cyrtiniform; dental adminicula and spondylium absent; ventral septum and dental flanges fused by apical callus or short transverse plate.

Stratigraphic Range.—Middle–Upper Triassic.

Subfamily Bittnerulinae Schuchert, 1929
[Subfamily Bittnerulinae Schuchert, 1929, p. 21]

Diagnosis.—Smooth or obscurely ribbed; fold and sulcus absent or very weak; delthyrium closed by convex deltidium.

Stratigraphic Range.—Middle–Upper Triassic.

Genera Included.—*Bittnerula* Hall and Clarke, 1895; *Leiolepismatina* Yang and Xu, 1966; *Thecocyrtella* Bittner, 1892; *Thecocyrtelloidea* Yang and Xu, 1966.

Subfamily Hirsutellinae Xu and Liu, 1983
[Subfamily Hirsutellinae Xu and Liu, 1983, p. 82]

Diagnosis.—Lateral slopes ribbed; fold and sulcus weakly to moderately developed; delthyrium open or partially occluded by various plates.

Stratigraphic Range.—Middle–Upper Triassic.

Genera Included.—*Hirsutella* Cooper and Muir-Wood, 1951; *Flabellocyrtia* Chorowicz and Termier, 1975; *Neocyrtina* Yang and Xu, 1966; *Spiriferinoides* Tokuyama, 1957.

Family Suessiidae Waagen, 1883
[*nom. trans.* Pitrat, 1965, p. H679
(*ex* Subfamily Suessiinae Waagen, 1883, p. 498)]

Diagnosis.—Entirely plicate; delthyrium open; dental adminicula and spondylium absent; large elongate hingeplate bearing adductors present.

Stratigraphic Range.—Lower Jurassic.

Genus Included.—*Suessia* Deslongchamps, 1855.

Superfamily Spondylospiroidea Hoover, 1991
[*nom. trans.* Carter, herein
(*ex* Family Spondylospiridae Hoover, 1991, p. 75)]

Diagnosis.—Spiriferiform to cyrtiniform; hingeline partially to completely crenulate; dental adminicula converging or forming spondylium; punctation well developed.

Discussion.—This compact group of 14 genera appeared cryptogenically in the Middle Triassic. Their unifying morphological character is the partially or completely crenulate hingeline. This articulatory structure has been termed "denticulate" by numerous authors but must be differentiated from the denticulate hingeline of the Spiriferoidea and Paleckelmanelloidea. In these groups the denticles consist of taleola-like rods embedded within secondary fibrous shell matter of the interareas. The crenulate teeth of the Spondylospioidea lack "taleolae" and are similar in each valve and interlocking. This is a unique or possibly synapomorphous articulatory structure among the spiriferinids.

This group includes both wide-hinged "spiriferoid" genera and hemipyramidal "cyrtinoid" genera. Internally, there is a good spondylium in the "cyrtinoid" genera or converging dental adminicula in the "spiriferoid" genera. The cyrtiniform spondylium-bearing genera are considered here to be most primitive and to indicate derivation from the laballids. The spiriferiform wide-hinged genera seem likely to have been derived from a cyrtiniform ancestor with neotenous loss of the complete spondylium and concomitant extension of the hingeline.

Stratigraphic Range.—Upper Triassic.

Family Spondylospiridae Hoover, 1991
[Family Spondylospiridae Hoover, 1991, p. 75]

Diagnosis.—Cyrtiniform to globose; lateral slopes ribbed; spondylium bisected by high median septum; jugum complete, supported by sessile jugal net.

Stratigraphic Range.—Middle (Ladinian)–Upper Triassic (Rhaetian).

Subfamily Spondylospirinae Hoover, 1991
[Subfamily Spondylospirinae Hoover, 1991, p. 80]

Diagnosis.—Dental adminicula and ventral interarea complete, not pierced by paired pedicle foramina.

Stratigraphic Range.—Upper Triassic (Karnian–Rhaetian).

Genera Included.—*Spondylospira* Cooper, 1942; *Phenacozugmayerella* Hoover, 1991; *Vitimetula* Hoover, 1991; *Yanospira* Dagis, 1977; *Zugmayerella* Dagis, 1963.

Subfamily Dagyspiriferinae Hoover, 1991
[Subfamily Dagyspiriferinae Hoover, 1991, p. 77]

Diagnosis.—Globose to cyrtiniform; entirely ribbed; apex of spondylium and ventral interarea pierced by paired elongate foramina.

Stratigraphic Range.—Upper Triassic (Karnian–Norian).

Genera Included.—*Dagyspirifer* Hoover, 1991; *Pseudospondylospira* Hoover, 1991.

Family Rastelligeridae Carter, **new family**

Diagnosis.—Spiriferiform; usually transverse; fold and sulcus smooth; lateral slopes usually plicate; dental adminicula subparallel or convergent.

Stratigraphic Range.—Middle–Upper Triassic.

Subfamily Rastelligerinae Carter, **new subfamily**

Diagnosis.—Strongly transverse; cardinal extremities extended; lateral slopes strongly plicate; dental adminicula convergent or forming sessile spondylium.

Stratigraphic Range.—Middle (Ladinian)–Upper Triassic (Rhaetian).

Genera Included.—*Rastelligera* Hector, 1879; *Boreiospira* Dagis, 1974; *Psioidiella* Campbell, 1968.

Subfamily Dentospiriferininae Carter, **new subfamily**

Diagnosis.—Cardinal extremities subangular to rounded; lateral slopes smooth or with few weak plicae; dental adminicula subparallel to convergent.

Stratigraphic Range.—Upper Triassic (Karnian–Norian).

Genera Included.—*Dentospiriferina* Dagis, 1965; *Canadospira* Dagis, 1972; *Orientospira* Dagis, 1965; *Psioidea* Hector, 1879.

Suborder Spiriferinidina Ivanova, 1972
[Suborder Spiriferinidina Ivanova, 1972, p. 41]
[=Suborder Spiriferinidina Cooper and Grant, 1976, p. 2666]

Diagnosis.—Subequally biconvex; ventral beak usually incurved; strong ventral median septum invariably present.

Discussion.—This suborder is presumed to have been derived from the cyrtinoid Family Komiellidae which had discrete dental adminicula in the Upper Devonian. Two distinct lineages appeared at this time. One formed the Pennospiriferinoidea with strong ventral median septum and leading to the highly successful radiation of similar genera in the Late Paleozoic and Triassic. The other lineage included large transverse genera bearing a strong delthyrial plate, the Syringothyridoidea. Although radically transformed internally, some of the advantages of the adductor-shortening structures of the cyrtinoid spondylium are retained in genera with a conical or hemipyramidal ventral valve, by the development of a simple high

median septum or large transverse delthyrial plate, respectively. In some moderately inflated, subequally biconvex syringothryridoid genera with low ventral interareas the delthyrial plate is lost, reflecting the lesser need for shortening the length of the adductors.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Lower Jurassic.

Superfamily Syringothyridoidea Frederiks, 1926
[*nom. correct.* Carter, herein (*pro* Syringothyridacea Frederiks, 1926 (*nom. imperf.*) *nom. trans.* Ivanova, 1972, p. 319, *ex* Syringothyrinae Frederiks, 1926, p. 411)]

Diagnosis.—Outline usually spiriferiform; moderately to strongly transverse; often strongly inequivalved; fold and sulcus invariably developed; lateral slopes with simple ribbing; micro-ornament consisting of fine short radial striae with fine elongate pustules or spinules arranged in quincunx between striae, producing textile-like appearance; dental adminicula present; cardinalia usually stout and wide; punctae highly variable in size, commonly sparsely and/or irregularly distributed.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Upper Permian.

Family Syringothrididae Frederiks, 1926
[*nom. correct.* Pitrat, 1965, p. H691 (*pro* Syringothyridae Frederiks, 1926 (*nom. imperf.*) *nom. transl.* Ivanova, 1959, p. 55, *ex* Syringothyrinae Frederiks, 1926, p. 411)]

Diagnosis.—Cardinal extremities subangular to slightly rounded; lateral slopes with moderately numerous simple ribs; interspaces narrow and subangular to moderately broad; fold and sulcus smooth medially; ventral interarea high to very high; perideltidial areas present.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Lower Permian.

Subfamily Syringothyridinae Frederiks, 1926
[*nom. correct.* Pitrat, 1965, p. H692 (*pro* Syringothyrinae Frederiks, 1926, p. 411)]

Diagnosis.—Delthyrial plate and syrinx present.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Lower Permian.

Genera Included.—*Syringothyris* Winchell, 1863 [=*Syringopleura* Schuchert, 1910]; *Subansiria* Sahni and Srivastava, 1956.

Subfamily Septosyringothyridinae Massa, Termier, and Termier, 1974
[*nom. correct.* Legrand-Blain, 1974, p. 120, *pro* Septosyringothyridae Massa, Termier, and Termier, 1974 (*nom. imperf.*) *nom. transl.* Carter, herein (*ex* Septosyringothyridae Massa, Termier, and Termier, 1974, p. 168)]

Diagnosis.—Median septum and syrinx present in ventral valve.

Stratigraphic Range.—Lower Carboniferous.

Genera Included.—*Septosyringothyris* Vandercammen, 1955; *Histosyrinx* Massa, Termier, and Termier, 1974.

Subfamily Permasyrinxinae Waterhouse, 1986
[Subfamily Permasyrinxinae Waterhouse, 1986, p. 3]

Diagnosis.—Syrinx absent.

Discussion.—The validity of *Pseudosyringothyris* Frederiks is in doubt. Grigor'eva (1977) states that intensive collecting for topotypes of *P. karpinskii* has failed to produce specimens internally similar to Frederiks's description of the type specimens. The presence of perideltidial areas in *Primorewia* Likharev and Kotljar has not been confirmed. If they are truly lacking, then *Primorewia* should be reassigned to the Licharewiidae.

Stratigraphic Range.—Lower Carboniferous (Lower Tournaisian)–Upper Permian.

Genera Included.—*Permasyrinx* Waterhouse, 1983; *Asyrinx* Hudson and Sudbury, 1959 [=*Kungaella* Solomina, 1988]; *Asyrinxia* Campbell, 1957; *Cyrtella* Frederiks, 1924 [=*Punctocyrtella* Plodowski, 1968]; *Myodelthyrium* Thomas, 1985; ?*Primorewia* Likharev and Kotljar, 1978; ?*Pseudosyringothyris* Frederiks, 1916; *Pseudosyrinx* Weller, 1914; *Sulcicosta* Waterhouse, 1983; *Verkhotomia* Sokolskaya, 1963.

Family Dimegelasmidae Carter, **new family**

Diagnosis.—Cardinal extremities well rounded; ventral interarea low to moderately high; lateral slopes with few plications separated by broad rounded interspaces; sulcus sparsely plicate or costate; perideltidial areas present; syrinx absent; delthyrial plate small or absent; shell substance thin.

Stratigraphic Range.—Upper Devonian (Famennian)–Lower Carboniferous (Visean).

Genera Included.—*Dimegelasma* Cooper, 1942 [=Doescherella Abramov and Grigor'eva, 1987]; *Guilinospirifer* Xu and Yao, 1988; *Zeugopleura* Carter, 1988.

Family Licharewiidae Slyusareva, 1958
[*nom. trans.* Solomina, 1988, p. 44
(*ex* Licharewiinae Slyusareva, 1958, p. 582)]

Diagnosis.—Perideltidial areas absent; syrinx absent; moderate to thick callus deposits in ventral umbonal region commonly present.

Discussion.—The presence or absence of perideltidial areas in *Pyramidathyris* Hu, *Tumarinia* Solomina and Grigor'eva, and *Tuotalania* Hu has not been demonstrated. The presence of such areas in any of these genera would require transfer to the Family Syringothyrididae.

Stratigraphic Range.—Upper Carboniferous–Upper Permian.

Genera Included.—*Licharewia* Einor, 1939 [=*Rugulatia* Sokolskaya, 1952]; *Olgerdia* Grigor'eva, 1977; *Orulgania* Solomina and Cherniak, 1961; *Penzhinella* Solomina, 1985; *Permospirifer* Kulikov, 1950; ?*Pyramidathyris* Hu, 1983; ?*Tumarinia* Solomina and Grigor'eva, 1973; ?*Tuotalania* Hu, 1983.

Superfamily Pennospiriferinoidea Dagis, 1972
[*nom. trans.* Carter, herein
(*ex* Subfamily Pennospiriferininae Dagis, 1972, p. 36)]

Diagnosis.—Spiriferiform to cyrtiniform; ventral interarea usually low or only moderately high; lateral slopes ribbed; dental adminicula and median septum discrete; punctae well developed, usually densely spaced.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Lower Jurassic.

Family Punctospiriferidae Waterhouse, 1975
[*nom. correct.* Carter, herein,
(*pro* Family Punctospiriferinidae Waterhouse, 1987, p. 44;

nom. trans. Waterhouse 1983 or 1987, *ex* Subfamily Punctospiriferinae Waterhouse, 1975, p. 17)]

Diagnosis.—Usually transverse; fold and sulcus narrow, weakly to moderately developed; dental adminicula short, subparallel to slightly divergent; micro-ornament capillate and usually regularly lamellose or subimbricate.

Discussion.—The faintly capillate micro-ornament in *Yangkongia* Xu and Liu is very poorly preserved and may in fact be an artifact of preservation. If so, reassignment would be necessary.

The earliest genus in this superfamily, *Ziganella* Nalivkin, has a low ventral median septum or ridge and normal fold-sulcus. This punctospiriferid genus is believed to have been derived from the Komiellidae or some intermediate ancestor within this lineage.

Stratigraphic Range.—Upper Devonian (Upper Famennian)–Middle Triassic.

Genera Included.—*Punctospirifer* North, 1920; *Alipunctifera* Waterhouse, 1975; *Lamnaespina* Waterhouse, 1976; *Liriplica* Campbell, 1961; *Pustulospiriferina* Waterhouse, 1983; ?*Yangkongia* Xu and Liu, 1983; *Ziganella* Nalivkin, 1960.

Family Spiropunctiferidae Carter, **new family**

Diagnosis.—Cardinal extremities well rounded; fold and sulcus plicate; micro-ornament absent.

Stratigraphic Range.—Lower Carboniferous (Upper Visean)–Upper Permian.

Genera Included.—*Spiropunctifera* Ivanova, 1971; *Genuspirifer* Liang, 1990.

Family Reticulariinidae Waterhouse, 1975
[*nom. trans.* Waterhouse, 1983, p. 138,
ex Subfamily Reticulariininae Waterhouse, 1975, p. 15]

Diagnosis.—Outline tranverse; cardinal extremities usually extended, rarely rounded; fold and sulcus narrow, usually well delimited; sulcus smooth or with weak median rib; dental adminicula divergent; micro-ornament of coarse hollow spines.

Stratigraphic Range.—Lower Carboniferous (Upper Visean)–Upper Permian.

Genera Included.—*Reticulariina* Frederiks, 1916; *Altiplecus* Stehli, 1954; *Gjelispinifera* Ivanova, 1975; *Spinuliplica* Campbell, 1961.

Family Paraspiriferinidae Cooper and Grant, 1976
[Family Paraspiriferinidae Cooper and Grant, 1976, p. 2729]

Diagnosis.—Outline transversely subelliptical; cardinal extremities well rounded; fold and sulcus usually well delimited; dental adminicula short, usually divergent; micro-ornament regularly and finely lamellose, with lamellae bearing fine hair-like spinules in some genera.

Stratigraphic Range.—?Lower Carboniferous (Upper Visean), Upper Carboniferous–Upper Permian.

Genera Included.—*Paraspiriferina* Reed, 1944; *Callispirina* Cooper and Muir-Wood, 1951; *Lamniplica* Waterhouse and Rao, 1989; *Polystylus* Klets, 1993; *Yaoniella* Waterhouse, 1983; *Zaissania* Sokoskaya, 1968.

Family Crenispiriferidae Cooper and Grant, 1976
[Family Crenispiriferidae Cooper and Grant, 1976, p. 2709]

Diagnosis.—Outline usually transversely subelliptical to subtrigonal; fold and sulcus usually narrow and poorly to moderately delimited; lateral slopes with few

strong lateral plicae and subimbricate growth varices; dental adminicula very short; micro-ornament finely pustulose.

Discussion.—*Tulungospirifer* Ching and Sun is tentatively assigned here on the basis of its growth form. Its micro-ornament differs from other genera in this family in having radial grooves and spinules.

Stratigraphic Range.—Lower Carboniferous (Upper Chesterian)–Upper Triassic.

Genera Included.—*Crenispirifer* Stehli, 1954; *Lancangjiangia* Jin and Fang, 1977; *Metriolepis* Cooper and Grant, 1976; *Pseudospiriferina* Young and Xu, 1966; *Spiriferellina* Frederiks, 1924 [=*Tylotoma* Grabau, 1934]; *Sulcispiriferina* Waterhouse and Gupta, 1981; ?*Tulungospirifer* Ching and Sun, 1976.

Family Sarganostegidae Cooper and Grant, 1976
[Family Sarganostegidae Cooper and Grant, 1976, p. 2743]

Diagnosis.—External surface with quincuntially arranged very coarse punctae; micro-ornament absent.

Stratigraphic Range.—Middle–Upper Permian.

Genus Included.—*Sarganostega* Cooper and Grant, 1969.

Family Balatonospiridae Dagis, 1974
[*nom. trans.* Carter, herein,
ex Subfamily Balatonospirinae Dagis, 1974, p. 137]
[=Subfamily Nudispiriferininae Xu and Liu, 1983]

Diagnosis.—Outline transversely subelliptical to subquadrate or subpentagonal; fold and sulcus poorly developed; entire surface usually ribbed.

Stratigraphic Range.—Middle–Upper Triassic.

Subfamily Yalongiinae Carter, **new subfamily**

Diagnosis.—Dental adminicula discrete.

Stratigraphic Range.—Middle Triassic.

Genera Included.—*Yalongia* Xu and Liu, 1983; *Aequispiriferina* Yang and Yin, 1962; *Sinucostella* Xu and Liu, 1983.

Subfamily Balatonospirinae Dagis, 1974
[Subfamily Balatonospirinae Dagis, 1974, p. 137]

Diagnosis.—Dental adminicula reduced or absent; dental flanges and median septum fused by transverse plate or callus.

Stratigraphic Range.—Middle (Anisian)–Upper (Karnian) Triassic.

Genera Included.—*Balatonospira* Dagis, 1974; *Dinarispira* Dagis, 1974; *Koeveskallina* Dagis, 1965; *Nudispiriferina* Yang and Xu, 1966; *Tylospiriferina* Xu, 1978.

Family Pennospiriferinidae Dagis, 1972
[*nom. trans.* Carter, herein,
ex Subfamily Pennospiriferininae Dagis, 1972, p. 36]

Diagnosis.—Transverse, usually with angular or extended lateral extremities; dental adminicula subparallel or converging; micro-ornament absent.

Stratigraphic Range.—Upper Carboniferous–Upper Triassic (Karnian), ?Lower Jurassic.

Subfamily Pennospiriferininae Dagis, 1972
[Subfamily Pennospiriferininae Dagis, 1972, p. 36]

Diagnosis.—Fold and sulcus smooth; dental adminicula converging, fused with median septum by thick callus.

Discussion.—The micro-ornament of *Callospiriferina* Rousselle, if any, is poorly known. Furthermore, the growth form of this genus differs substantially from that of the type genus.

Stratigraphic Range.—Middle Triassic (Ladinian)–?Lower Jurassic.

Genera Included.—*Pennospiriferina* Dagis, 1965; ?*Callospiriferina* Rousselle, 1977.

Subfamily Punctospirellinae Dagis, 1974
[Subfamily Punctospirellinae Dagis, 1974, p. 135]
[=Family Xestotrematidae Cooper and Grant, 1976, p. 2748]

Diagnosis.—Fold and sulcus smooth or weakly ribbed; dental adminicula discrete, usually short, not converging.

Discussion.—This long-ranging subfamily, if it proves to be monophyletic, is probably the ancestral stock for the other Triassic families in this superfamily.

Stratigraphic Range.—Upper Carboniferous–Middle Triassic.

Genera Included.—*Punctospirella* Dagis, 1974; *Arionthia* Cooper and Grant, 1976; *Laioporella* Ivanova, 1975; *Xestotrema* Cooper and Grant, 1969 [=*Mucrospiriferinella* Waterhouse, 1982].

Family Lepismatinidae Xu and Liu, 1983
[Family Lepismatinidae Xu and Liu, 1983, p. 82]

Diagnosis.—Cyrtiniform or globose; lateral slopes ribbed; fold and sulcus well developed; delthyrium open; dental adminicula discrete.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Subfamily Lepismatininae Xu and Liu, 1983
[*nom. trans.* Carter, herein,
ex Family Lepismatinidae Xu and Liu, 1983, p. 82]

Diagnosis.—Fold and sulcus smooth; micro-ornament of dense spinules; cardinalia sessile.

Stratigraphic Range.—Middle–Upper Triassic.

Genera Included.—*Lepismatina* Wang, 1955 [=*Costispiriferina* Dagis, 1974]; *Altoplicatella* Xu and Liu, 1983; *Pseudolepismatina* Ching and Sun, 1976.

Subfamily Pseudocyrtininae Carter, **new subfamily**

Diagnosis.—Fold and sulcus smooth; cardinalia supported by short median septum; micro-ornament absent.

Stratigraphic Range.—Upper Triassic.

Genera Included.—*Pseudocyrtina* Dagis, 1962; *Bolilaspirifer* Sun, 1981.

Subfamily Dispiriferininae Carter, **new subfamily**

Diagnosis.—Entirely ribbed; no dorsal septum.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Genera Included.—*Dispiriferina* Siblik, 1965; *Qingyenia* Yang and Xu, 1966.

Superfamily Spiriferinoidea Davidson, 1884
[*nom. correct.* Carter, herein (*pro* Superfamily Spiriferinacea Davidson, 1884 (*nom. imperfect.*) *nom. trans.* Ivanova, 1959, p. 57, *ex* Subfamily Spiriferininae Davidson, 1884, p. 354)]

Diagnosis.—Reticulariiform, subequally biconvex; cardinal extremities well rounded; ventral beak incurved; fold and sulcus usually weakly developed; lateral slopes smooth or obscurely ribbed, rarely with moderately developed ribbing.

Discussion.—The growth form, internal morphology, and micro-ornament of this superfamily strongly suggest that it was derived from some member of the Family Paraspiriferinidae.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Family Spiriferinidae Davidson, 1884
[*nom. trans.* Ivanova, 1959, p. 57 (*ex* Subfamily Spiriferinidae Davidson, 1884, p. 354)]

Diagnosis.—Lateral slopes smooth or obscurely ribbed.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Subfamily Spiriferininae Davidson, 1884
[Subfamily Spiriferinidae Davidson, 1884, p. 354]
[=Subfamily Spiriferellinae Paeckelmann, 1932, p. 25, *pro* Spiriferininae Schuchert, 1929, p. 21]

Diagnosis.—Reticulariiform; dental adminicula discrete.

Stratigraphic Range.—Middle Triassic–Lower Jurassic.

Genera Included.—*Spiriferina* Orbigny, 1847 [=*Liospiriferina* Rouselle, 1977]; *Calyptoria* Cooper, 1989 [=*Cingolospiriferina* Pozza, 1992]; *Mentzelioides* Dagis, 1974; *Qinghaispiriferina* Sun and Ye, 1982; *Triadispira* Dagis, 1961; *Viligella* Dagis, 1965.

Subfamily Paralaballinae Carter, **new subfamily**

Diagnosis.—Cyrtiniform; fold and sulcus weakly developed; ornament absent; dental adminicula discrete, thin, short, subparallel.

Stratigraphic Range.—Upper Triassic.

Genus Included.—*Paralaballa* Sun, 1981.

Subfamily Mentzeliinae Dagis, 1974
[Subfamily Mentzeliinae Dagis, 1974, p. 138]

Diagnosis.—Dental adminicula absent.

Stratigraphic Range.—Middle–Upper Triassic.

Genera Included.—*Mentzelia* Quenstedt, 1871; *Madoia* Sun and Ye, 1982; *Paramentzelia* Xu, 1978.

Subfamily Tethyspirinae Carter, **new subfamily**

Diagnosis.—Spondylium present.

Stratigraphic Range.—Middle (Ladinian)–Upper (Karnian?) Triassic.

Genera Included.—*Tethyspira* Siblik, 1991; *Spondylospiriferina* Dagis, 1972.

Family Sinucostidae Xu and Liu, 1983
[*nom. trans.* Carter, herein, *ex* Subfamily Sinucostinae Xu and Liu, 1983, p. 112]

Diagnosis.—Lateral slopes ribbed; dental adminicula discrete.
Stratigraphic Range.—Middle–Upper Triassic, ?Lower Jurassic.

Subfamily Sinucostinae Xu and Liu, 1983
[Subfamily Sinucostinae Xu and Liu, 1983, p. 112]

Diagnosis.—Dorsal septum absent.
Stratigraphic Range.—Middle–Upper Triassic, ?Lower Jurassic.
Genera Included.—*Sinucosta* Dagis, 1963 [=*Guseriplica* Dagis, 1963]; *Mentzeliopsis* Trechmann, 1918; *Qispiriferina* Xu and Liu, 1983.

Subfamily Jiangdaspiriferinae Carter, **new subfamily**

Diagnosis.—With dorsal median septum.
Stratigraphic Range.—Upper Triassic.
Genus Included.—*Jiangdaspirifer* Chen, Rao, Zhou, and Pan, 1986.

Suborder uncertain
Superfamily uncertain
Family uncertain

Genus Included.—*Plicatosyrinx* Minato, 1952.

REJECTED FROM THE SPIRIFERS

Genera Included.—*Guangshunia* Xian 1978 [possible stringocephalid]; *Iliella* Rukavischnikova 1980 [Ashgill, not an *Eospirifer*]; *Plectospirifer* Grabau, 1931 [its type species is a synonym of *Athyrisina squamosa* Hayasaka, type species of *Athyrisina*]; *Pustulatia* Cooper 1956 [possible anoplothecid]; *Xerxespirifer* Cocks 1979 [rhynchonellid or leptocoeliid].

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APPENDIX

Boucot (1973:39–61; 1975:369–370) used the term "ctenophoridium" for the striate site of dorsal diductor attachment in some spiriferid brachiopod genera, but did not define the term. We remedy that oversight here and call attention that "ctenophoridium" will appear as an accepted usage in the glossary of the forthcoming revision of the brachiopod Treatise. Krans (1965:pl. 16) illustrated thin sections of the ctenophoridium, which he refered to as a cardinal process of *Cyrtospirifer* and an unidentified genus.

ctenophoridium.—Striated or comb-like site of dorsal diductor muscle attachment situated on floor of notothyrial cavity or bifid on hinge plates, but not elevated on a shaft-like cardinal process.

LITERATURE CITED

To include here every dated citation given above would require the editors to print many pages of text in addition to an already long paper. Therefore, we exclude references for the taxonomic units and list here only those papers cited in the text. Readers who wish to obtain citations for a particular taxon may call, write, or e-mail Carter. Carter's e-mail address is: JLC4@VMS.CIS.PITT.EDU; telephone (412) 622-3263.

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